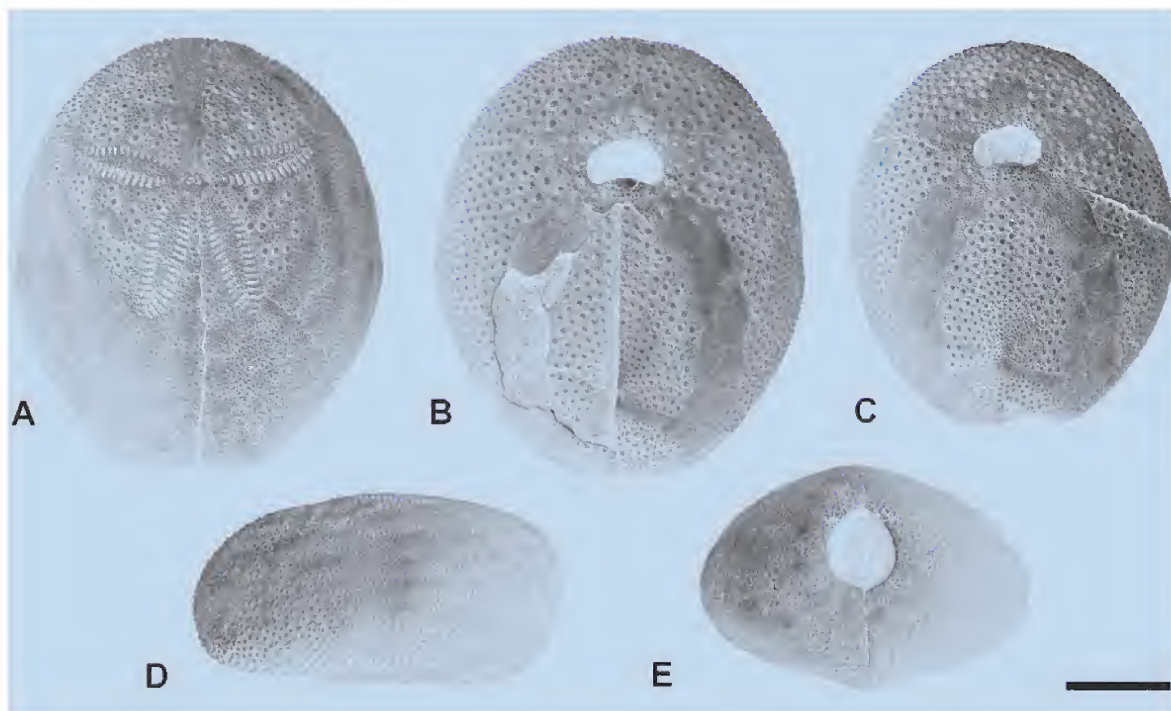
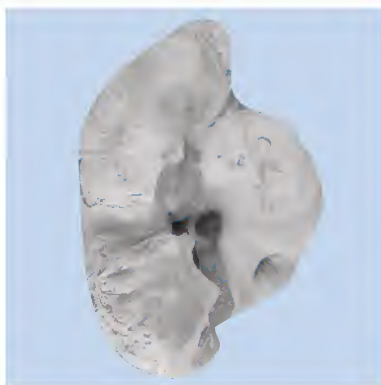
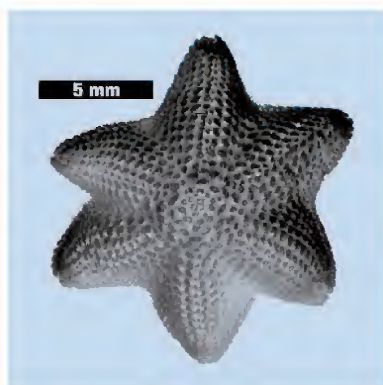


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Front cover Top left: a new species of seastar from Mauritius, *Ailsastra eleaumei*, described by P. Mark O'Loughlin and Francis W.E. Rowe. Top centre: an earbone of a fossil dolphin of the family Delphinidae from the Pliocene Whalers Bluff Formation, Portland, Victoria, described by Erich M. G. Fitzgerald. Bottom: a new species of fossil sea urchin, *Spatagobrissus dermodyorum*, described by Francis Holmes from the early Middle Miocene Glenforslan Formation near Blanchetown, South Australia. Back cover: male reproductive organs of a new species of millipede, *Lissodesmus dignomontis*, from Tasmania, described by Robert Mesibov.

Homalonotid trilobites from the Silurian and Lower Devonian of south-eastern Australia and New Zealand (Arthropoda: Trilobita: Homalonotidae)

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Abstract

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Trilobites belonging to the Homalonotidae are well represented in the Silurian and Early Devonian of south-eastern Australia and New Zealand, and are a significant component of the family world-wide. Their description provides an opportunity to review relationships between species and higher order taxa. A new genus *Wenndorfia* and two new subgenera *Trimerus* (*Ramiotis*) and *T.* (*Edgillia*) are described, and revised diagnoses are given for *Trimerus*, *Homalonotus*, *Dipleura*, *Digonus* and *Parahomalonotus*. Species described or redescribed from central Victoria include *Homalonotus williamsi* sp. nov., *H. talenti* sp. nov., *Dipleura garratti* sp. nov., *Digonus wenndorfi* sp. nov., *Trimerus* (*Trimerus*) *vomer* (Chapman, 1912), *T.* (*T.*) *harrisoni* (McCoy, 1876), *T.* (*Edgillia*) *kinglakensis* (Gill, 1949), *T.* (*E.*) *jelli* sp. nov., *T.* (*Ramiotis*) *rickardsi* sp. nov., *T.* (*R.*) *tomczykowa* sp. nov., *T.* (*R.*) *otisi* sp. nov., *T.* (*R.*) *thomasi* sp. nov. and *Wenndorfia lilydalensis* (Gill, 1949). Tasmanian species described include *T.* (*R.*) *iani* sp. nov., *Brongniartella*? sp. and *D. zeehanensis* (Gill, 1949). *Wenndorfia expansa* (Hector, 1876) (= *H. (Burmeisteria) huttoni* Allan, 1935, = *D. margaritifera* Wenndorf, 1990) from New Zealand is redescribed.

Complex relationships between trilobite faunal composition and taphonomy demonstrate that homalonotid assemblages are inadequately described by the biofacies concept. A recurrent relationship can be recognised between homalonotid-dominated low diversity assemblages and high diversity assemblages in relatively shallower-water facies in which homalonotids are minor faunal elements. These paired assemblages occur variously along a bathymetric gradient that reflects specific environmental tolerances, and precludes the definition of discrete assemblage-facies associations.

Keywords

Trilobita, Homalonotidae, Silurian, Devonian, Australia, New Zealand, systematics, biofacies

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Introduction

Homalonotid trilobites were first recorded from south-eastern Australia and New Zealand as early as the 1860s, and eight species have been described subsequently including *Homalonotus expansus* Hector, 1876, *H. harrisoni* McCoy, 1876, *H. (Burmeisteria) huttoni* Allan, 1935, *Trimerus lilydalensis* Gill, 1949, *H. vomer* Chapman, 1912, *T. kinglakensis* Gill, 1949, *T. zeehanensis* Gill, 1949 and *Digonus margaritifera*

Wenndorf, 1990. The relationships of these taxa have been poorly understood, as most of them were inadequately described from limited populations and/or poorly preserved or incomplete individuals. Museum Victoria houses a large collection of homalonotid specimens from Australasia which not only permits the redescription of these species, but also the description of many new species.

Both in taxonomic diversity and abundance the homalonotid fauna of south-eastern Australia is of world-wide significance. It is undoubtedly the best preserved representation of the family for the Llandovery to Lochkovian interval, representing about one-third of species so far described (Table 1). Three Llandovery species bring to eight the total number of homalonotids recorded from the interval, with two of them being among the three best known taxa. Seven Victorian Ludlow species bring to 15 the total number of homalonotids recorded from that interval. Similarly, four Lochkovian species make up one-quarter of the total number of homalonotids recorded from that interval. The species assigned below to *Homalonotus* are two of the total of five assigned to that genus globally, whilst the nine species assigned below to *Trimerus* represent almost half of the species assigned to that genus. A species assigned to *Dipleura* is the earliest known representative of the genus, and two species assigned to *Digonus* are among the earliest representatives of that genus.

Historically, the systematics of the Homalonotidae has been heavily weighted towards the classification of European and North American species that represent about two-thirds the total number of species so far described. This trend persists in the two most recent taxonomic revisions accompanying the description of north European faunas (Tomczukowa, 1975; Wenndorf, 1990). In contrast and with the exception of *Burmeisteria*, species from Asia, North Africa and the southern hemisphere have been accommodated in taxa established for the European and North American faunas. However, problems arise with the uncritical application of generic concepts established for European and North American faunas to the classification of southern hemisphere homalonotids, and are manifest in the nomenclatural changes suffered by some of the few well documented species. *Homalonotus clarkei* Kozłowski, 1923 from the Devonian of Brazil has been variably assigned to *Digonus* (Wolfart et al., 1968), *Trimerus?* (Tomczukowa, 1975), *Burmeisteria* (Cooper, 1982), and *Dipleura* (Wenndorf, 1990). Similarly, *B. (Digonus) accraensis* Saul, 1967 from the Devonian of Ghana has been variably assigned to *Trimerus* (Tomczukowa, 1975), *Burmeisteria* (Cooper, 1982) and *Dipleura?* (Wenndorf, 1990). The comprehensive redescription of the Australian homalonotid fauna in this work documents a morphological diversity that demands a more critical usage of established generic concepts. Revised diagnoses are given in this work for *Homalonotus*, *Digonus*, *Parahomalonotus*, *Dipleura* and *Trimerus* to accommodate the morphological diversity of the Australasian fauna.

The Australasian fauna provides new perspectives on the relationships between species. *Trimerus* is well represented in the Australian fauna with nine species assigned to the genus. The relationships between these and other species of the genus are formalised in the description of the new subgenera *Ramiotis*

and *Edgillia*. *T. lilydalensis* from Victoria shows closest relationships to European species previously assigned to *Parahomalonotus*. The new genus *Wenndorfia* is erected to accommodate *T. lilydalensis* and these closely related taxa, and the concept of *Parahomalonotus* is revised and restricted to those species close to the type. Reassignment of species to these groups (Table 1) reflects these revised concepts.

The Silurian and to a lesser extent the Early Devonian are generally considered periods of cosmopolitanism, and this is reflected in the widespread distribution of species groups and higher taxa. Although restricted to the late Wenlock-early Ludlow, *Trimerus* (*Trimerus*) is represented in North America, South America, Europe and Australia, with *T. (T.) vomer* from Victoria and *T. (T.) johannis* Salter, 1865 from England defining a distinct trans-global species group. *Wenndorfia lilydalensis* from the early Pragian of Victoria is closest to poorly known species from the late Lochkovian of Europe. The morphological diversity present in the Australian fauna is more a reflection of the age of the fauna rather than its palaeogeographic setting. Most of the Australian species are from the Llandovery, Ludlow and Lochkovian intervals in which many of the species documented from elsewhere are poorly understood and have had little influence on systematics. *Trimerus* (*Edgillia*) is erected for a distinct group of globally distributed Prídolí-early Lochkovian species typified by *T. (E.) kinglakensis* from central Victoria but otherwise very poorly represented in the fossil record. Similarly, *T. (Ramiotis)* is erected for a widespread group of Llandovery-Ludlow species poorly represented in the fossil record outside Australia. Siluro-Devonian homalonotid groups not represented in Australia and New Zealand include *Parahomalonotus*, *Burmeisteria*, *Burmeisterella*, *Scabrella* and *Arduenella*.

Geological Setting

In central Victoria, trilobite-bearing Silurian to Lower Devonian marine sedimentary rocks of the Murrumbidgee Supergroup crop out in a structurally bound area known as the Melbourne Zone (VandenBerg et al., 2000). Lithologies are predominantly interbedded mudstones, siltstones and fine to medium-grained sandstones, although coarse sandstones and conglomerates occur at various horizons. Carbonates, known only from the Lower Devonian in the central and eastern areas of the Melbourne Zone, are poorly represented and occur as isolated, discrete limestone bodies.

Homalonotids are restricted in distribution to non-carbonate sequences between Melbourne, Heathcote and Lilydale in the western and central areas of the Melbourne Zone (Fig. 1). The lithostratigraphy of these homalonotid-bearing sequences has been variously described. The definition, correlation and age of the various trilobite-bearing lithostratigraphic units described from these sequences has been reviewed by Rickards and Sandford (1998) and Sandford (2000, 2002, 2003, 2004). Stratigraphic nomenclature for the Llandovery to early Ludlow sequence used in this work (Fig. 2) follows Rickards and Sandford (1998: fig. 2) and Sandford (2000: fig. 2), and that for the overlying Ludlow to Pragian sequences follows Sandford (2002, fig. 2). Homalonotids first appear in the latest

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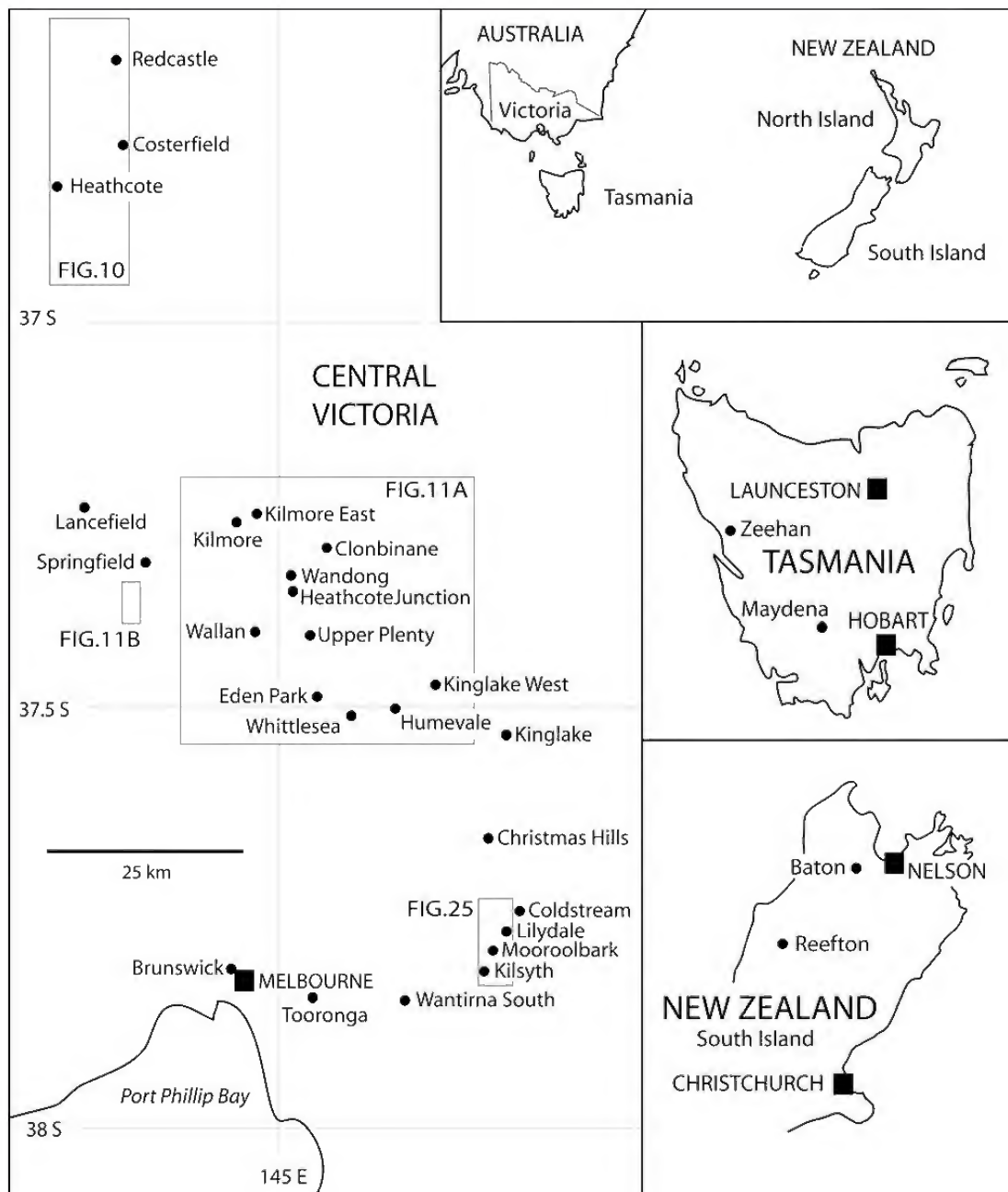


Figure 1. Distribution of fossil marine faunas with homalonotids in south eastern Australia and New Zealand. Localities for the Heathcote, Springfield-Kinglake West and Lilydale areas are detailed in Figures 8, 11 and 23.

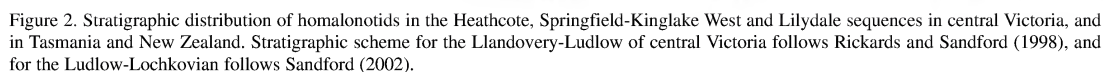


Figure 2. Stratigraphic distribution of homalonotids in the Heathcote, Springfield-Kinglake West and Lilydale sequences in central Victoria, and in Tasmania and New Zealand. Stratigraphic scheme for the Llandovery-Ludlow of central Victoria follows Rickards and Sandford (1998), and for the Ludlow-Lochkovian follows Sandford (2002).

Llandovery Chintin Formation at Springfield and occur at various horizons in the overlying sequences, ranging high in the Mt Ida Formation at Heathcote in strata considered to be late Lochkovian in age, and ranging up to the top of the Humevale Formation at Lilydale in strata considered to be early Pragian in age. Homalonotids do not occur in the various Lochkovian-Pragian trilobite faunas from the western areas of the Melbourne Zone, east of Lilydale. Silurian-Early Devonian sequences occur widely in Tasmania, but homalonotids are known only from the south-western areas, in the Llandovery Richea Siltstone northwest of Maydena and in the Lochkovian Bell Shale at Zeehan. On the south island of New Zealand, homalonotid trilobites are known from the Lochkovian-?Pragian Baton Formation, Baton River and from the ?Pragian-Emsian Lankey Limestone at Reefton.

Silurian and Devonian trilobite faunas occur widely across the eastern states of Australia, and the restricted distribution of homalonotids to the south-western areas of the Melbourne Zone and to south-western Tasmania is noteworthy. Acastid trilobites are similarly distributed, whereas the distribution of harpetid trilobites complements that of the homalonotids and acastids, ranging from eastern Victoria to northern Queensland. The limited distribution of homalonotids in eastern Australia parallels their distribution in Europe across the Rheinischen-Bohemischen facies boundary. The barrier to dispersal in eastern Australia is not apparent for other trilobites, particularly the phacopids and the calymenids. *Echidnops*, the *Ananaspis typhlagogus* (Öpik, 1953) species group and individual species such as *Sthenarocalymene* sp. A of Chatterton, Johnson and Campbell, 1979 are represented both in central Victoria and New South Wales. It is currently held that the sequences of the Melbourne Zone were deposited on a low gradient shelf on the eastern margin of the Australian continental plate. In contrast, the sequences in eastern Victoria, New South Wales and Queensland were deposited on off-shore island-arc platforms many hundreds of kilometres from the mainland (Foster et al., 1999). It seems that although many trilobite groups were able to establish themselves in these settings, homalonotids (and acastids) were unsuccessful in dispersing from the continental margin. Isolation of the homalonotids can be attributed to preferences for continental margin environments.

Taphonomy and biofacies

The homalonotid-bearing trilobite faunas from the Silurian and Lower Devonian of central Victoria are quite variable in taxonomic composition and relative abundance of species, taphonomy, associated lithofacies and associated non-trilobite faunal elements. Several faunas can be assigned to homalonotid-dominated biofacies including the Homalonotid Association (Mikulic, 1999), the *Trimerus delphinocephalus*-*Dalmanites limulurus* Association (Mikulic, 1999) and the *Digonus* Biofacies (Fortey and Owens, 1997). Other faunas resemble the *Acaste*-*Trimerus* Association (Thomas, 1979).

Mikulic (1999) emphasised trilobite elements of Boucot's (1975) shallow water 'Homalonotid-*Plectonotus* BA-1 Community' in defining the Homalonotid Association. Mikulic nominated the low diversity/monospecific Ludlow assemblages

dominated by *Homalonotus dawsoni* Hall, 1860 of the Stonehouse Formation, Arasaig, Canada as typical. The biofacies is associated with coarse- to fine-grained siliciclastics of nearshore environments and a taphonomy dominated by disarticulated exoskeletal elements. Mikulic assigned faunas ranging worldwide from the Caradoc through to the Givetian to the Homalonotid Association. Taxa commonly associated with this assemblage include *Acaste*, *Acastella*, *Encrinurus*, *Scotiella*, *Dalmanites* and calymenids. The Homalonotid Association can be recognised in the Upper Silurian-Lower Devonian sequences at Heathcote in central Victoria, represented by populations of *Homalonotus talenti* sp. nov., *Trimerus* (*Ramiotis*) *thomasi* sp. nov. and *Digonus wenndorfi* sp. nov. at successive horizons. Most typical is the mono-specific assemblage at the type locality of *H. talenti* (PL6650, Heathcote). The population is preserved in thick-bedded coarse sandstones of the McIvor Formation and is represented predominantly (94%) by isolated sclerites. At its type locality (PL2203, Heathcote), the population of *D. wenndorfi* is represented entirely by isolated sclerites. The species occurs in medium to coarse sandstones of the Mt Ida Formation in association with rare *Acastella* sp. and an abundance of very large bivalves and brachiopods (Fig. 3). The latter indicate alignment of the fauna to the 'big-shell community' of Boucot and Johnson (1967), later formally designated benthic assemblage BA-1 (Boucot, 1975) and interpreted to be a very shallow-water community. The *D. wenndorfi* fauna at PL2203 can also be assigned to the *Digonus* Biofacies of Fortey and Owens (1997). The *Digonus* Biofacies was recognised as the shallowest in a succession of depth-related trilobite associations of Early Devonian shelf environments, with deeper associations named after their characteristic key taxa *Scutellum*, *Lepidoproetus*, *Odontochile* and *Otarion*. Although Fortey and Owens did not provide any description of these associations, their scheme follows Chlupáč's (1983, 1987) depth-related succession of lithofacies and trilobite associations described from the Czech sequences as Major Assemblage Groups I-V. The association of *Digonus*, *Acastella* and an abundance of bivalves at PL2203 also resembles Thomas' (1979) *Trimerus-Acaste* Association, described from shallow water facies of the British Wenlock. The *Trimerus-Acaste* Association can be regarded as the Silurian equivalent of the Devonian *Digonus* Biofacies, both considered here as synonyms of the Homalonotid Association.

Low diversity trilobite faunas with species of *Trimerus* and *Dalmanites* (or *Odontochile*) as the two dominant taxa occur at successive horizons in deeper-water sequences south of Heathcote. An earliest Ludlow fauna from PL386, Wandong is dominated by an association of *D. wandongensis* Gill, 1948 and *T. (T.) vomer*. The fauna is preserved in siltstones as isolated sclerites and partly disarticulated exoskeletons, some of which represent moult assemblages and indicate a depositional environment below storm wave base (Sandford, in press). A late Ludlow fauna from PL1898, Eden Park is similarly preserved, dominated by *T. (Ramiotis) otisi* sp. nov. (relative abundance 96%) with rare *Odontochile formosa* Gill, 1948 (relative abundance 4%). A late Lochkovian fauna from the upper massive siltstone beds at Middendorps Quarry (PL252, Kinglake West)



Figure 3. Sandstone slab from PL2204 (Thomas' F4, Parish of Dargile), Heathcote with bedding plane showing numerous isolated pygidia and cranidia of *Digonus wenndorfi* in various orientations and with large bivalves and brachiopods indicative of Boucot and Johnson's (1967) 'big shell' community.

is dominated by *T. (Edgillia) kinglakensis* (relative abundance 99%) with rare *O. formosa*. These assemblages can be assigned to the *T. delphinocephalus*-*D. limulurus* Association, typified by a trilobite fauna dominated by these taxa from the Wenlock Rochester Shale, USA. Mikulic (1999) interpreted the community as a deeper-water facies association, preserved as disarticulated exoskeletons in fine-grained, deep water/low energy siliciclastics and aligned with BA 4 and BA 5 communities, Brett's (1983) *Amphistrophia*-*Dalmanites* Community in particular. Mikulic (1999) tentatively assigned assemblages occurring in shallower facies (BA3) to the *T. delphinocephalus*-*D. limulurus* Association. Equivalent shallower assemblages in central Victoria include the *O. formosa*-dominated fauna from the lower coquina siltstones and sandstones at Middendorps Quarry, in which *T. (E.) kinglakensis* is rarer.

At a number of localities in the uppermost Humevale Siltstone at Lilydale *Wenndorfia lilydalensis* occurs with *Acastella frontosa* Shergold, 1968, often as dominant elements of the fauna. These faunas resemble Thomas' (1979) *Trimerus*-*Acaste* Association, although the facies at Lilydale suggest a deeper-water setting. Another acastid, *Acaste lokii* Edgecombe,

1993, occurs lower in the Humevale Siltstone in the Lilydale area, its stratigraphic range overlapping with that of *W. lilydalensis*, but the two species never occur together.

Despite the recognition of homalonotid biofacies at several localities, the homalonotid faunas of south-eastern Australia are otherwise inadequately described by the biofacies concept. Patterns can be recognised demonstrating more complex relationships between homalonotid relative abundance, faunal diversity, taphonomy and lithofacies. A skewed inverse relationship between relative abundance and faunal diversity can be demonstrated, with lower diversity trilobite associations having homalonotids proportionally over-represented, and higher diversity associations with homalonotids under-represented. In the higher diversity faunas, dalmanitids or proetids are frequently the dominant taxon, although acastids, phacopids and rarely odontopleurids may also dominate. The relationships between taxonomic diversity and homalonotid relative abundance is best expressed graphically (Fig. 4).

Several species from central Victoria including *Digonus wenndorfi*, *Trimerus (Edgillia) kinglakensis*, *T. (Ramiotis) otisi* and *Wenndorfia lilydalensis* are known from both low

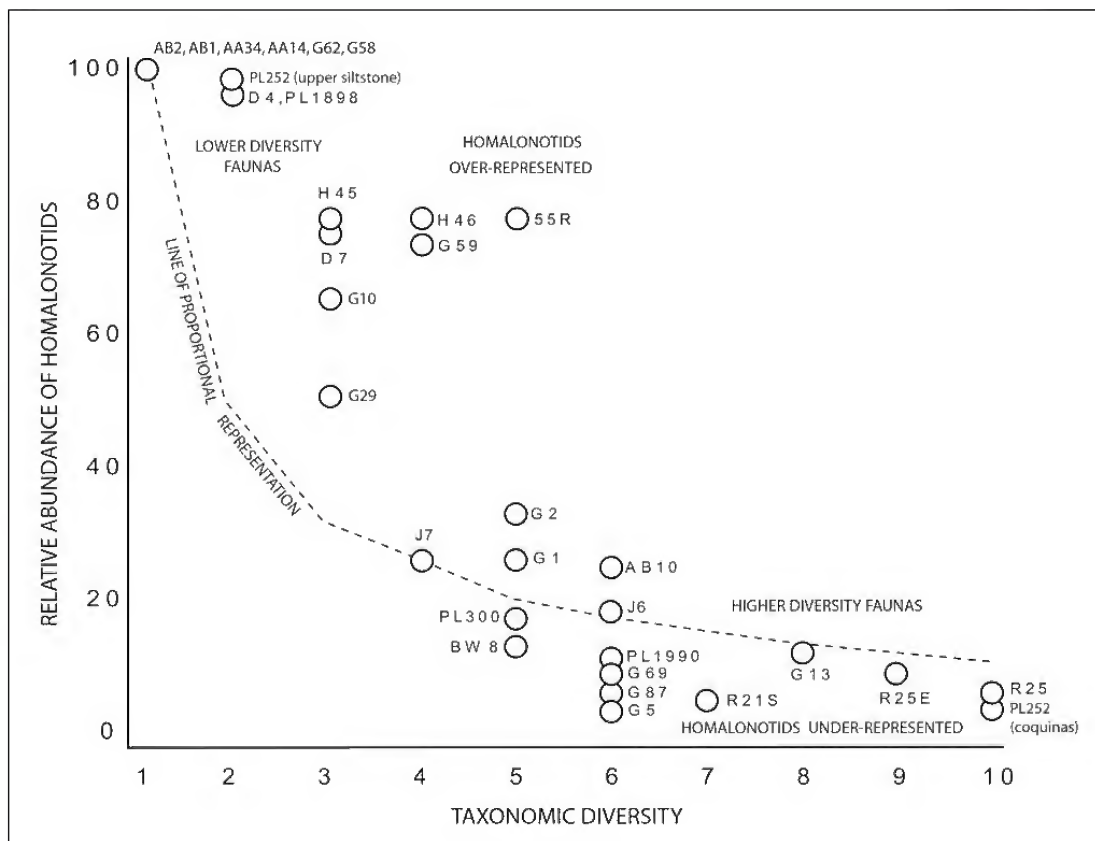


Figure 4. Relationship between trilobite faunal diversity and homalonotid relative abundance. Only homalonotid-bearing faunas represented by more than 10 specimens are plotted. The curve connects plot-points of hypothetical faunas where species are represented in equal proportional relative abundance. Homalonotid faunas cluster in two groups, lower diversity faunas with homalonotids over-represented (above the line) and high diversity faunas with homalonotids generally under-represented (below the line).

diversity, homalonotid-dominated assemblages and high diversity assemblages in which homalonotids are under-represented. From these occurrences, a pattern emerges revealing a relationship between trilobite assemblage composition, taphonomy and lithofacies (Table 2). This relationship is best illustrated in the distribution of *T. (E.) kinglakensis* in the upper massive siltstones and the lower bedded coquinal siltstones and sandstones at Middendorps Quarry, where a marked contrast in facies accompanies differences in faunal composition. In the upper beds *T. (E.) kinglakensis* is extremely dominant (relative abundance 99%) in a low-diversity assemblage accompanied by rare *Echidnops hollowayi* Sandford, 2002 and *Odontochile formosa*. Individuals are preserved predominantly as partly articulated and frequently incomplete exoskeletons or otherwise as isolated pygidia. Despite the exceptionally high proportion of partly articulated exoskeletons, complete fully articulated exoskeletons are absent. Many of the partly articulated

exoskeletons can be interpreted as moult assemblages, preserved in typical phacopid fashion with the cephalon displaced, often inverted and/or lying underneath the thoracopygon (Figs 5A, 5D). Partly-articulated thoraxes can be interpreted as elements of moult assemblages scattered by the movements of the animal during the exuvial process. Indeed, it is probable that the whole population of *T. (E.) kinglakensis* in the massive siltstones (including the isolated cephalae and pygidia) are derived from exuviae rather than dead individuals.

Well bedded, siltstones and graded sandstones with poorly sorted, bioclastic basal coquinal lags underlie the siltstones at Middendorps Quarry and yield a much more abundant and diverse benthic fauna. By world standards ten taxa is low diversity for an Early Devonian trilobite assemblage, but for central Victoria this is one of the most diverse. The assemblage is dominated by *Lepidoproetus* sp. and *Odontochile formosa* with a combined relative abundance of 64%. *Trimerus* (*Edgillia*)

Table 2. Relationships between lithology, relative abundance and taphonomy for *Trimerus (Edgillia) kinglakensis*, *Trimerus (Ramiotis) otisi* and *Wenndorffia lilydalensis*. Populations of the latter species in the Eden Park and Humevale siltstones are taken as a whole.

	<i>Trimerus (Edgillia) kinglakensis</i> Humevale Formation PL252 (type locality)		<i>Trimerus (Ramiotis) otisi</i> Eden Park Formation		<i>Wenndorffia lilydalensis</i> Humevale Formation	
LITHOLOGY	siltstone	coquina	siltstone	coquina	siltstone (Clonbinane Sandstone Member: PL300, PL6642)	coquina (PL1804)
TOTAL specimens	286	15	132	8	58	1
RELATIVE ABUNDANCE	99%	15%	96%	24%	26%	2%
TAPHONOMY						
complete dorsal exoskeleton	0	40%	1%	36%	0	100%
cephalothorax	<1%	0	1.5%	13%	2%	0
cephalon with displaced thoracopygon	12%	0	2%	0	2%	0
cephalon with displaced thorax	10%	0	1.5%	0	0	0
cephalon with displaced thorax and displaced pygidium	1%	0	0	0	0	0
cephalon	11%	0	11%	0	17%	0
isolated cranidium	<1%	0	17%	0	12%	0
isolated librigena	0	0	2%	0	5%	0
isolated hypostome	0	0	1%	0	0	0
articulated/partly articulated thorax	9%	0	6%	0	0	0
loosely disarticulated thorax	<1%	0	0	0	0	0
isolated thoracic segment	0	0	2%	13%	21%	0
partly disarticulated thorax, displaced pygidium	3%	0	0	0	0	0
complete/partly complete thoracopygon	36%	0	7%	13%	0	0
isolated pygidium	15%	60%	48%	25%	41%	0
articulated/partly articulated specimens	84%	40%	70%	75%	21%	100%
TAPHOFACIES	TIV	THH	TIV	THH	TIV	THH

kinglakensis is a minor faunal element (relative abundance <3%). In further contrast to its representation in the overlying siltstones, the population of *T. (E.) kinglakensis* in the coquinas has a high proportion (13%) of complete, fully articulated exoskeletons. Populations of other species in these beds also have a high proportion of complete exoskeletons, including *Lepidoproetus* sp. (42%), *Maurotarion* sp. (33%), *Echidnops hollowayi* (21%), *Leonaspis* sp. (11%) and *Dicranurus kinglakensis* Gill, 1947 (6%).

Similar relationships between faunal composition and taphonomy can be demonstrated for *Trimerus (Ramiotis) otisi* and *Wenndorffia lilydalensis*. The single known complete exoskeleton of *W. lilydalensis* from PL1804, Coldstream is exceptional in several respects. It occurs in a bioclastic coquina lag within a fine-grained sandstone (Fig. 5C), identical to the style of preservation of *T. (Trimerus) harrisoni* at PL1820, West Brunswick (Fig. 5B) where most specimens (58%) are complete exoskeletons. The relative abundance of *W. lilydalensis* at PL1804 is very low (2%), exceptionally under-represented in an assemblage of relatively high diversity (8 species). By contrast, all other specimens of the species

including isolated tergites and partly disarticulated exoskeletons occur in thick-bedded siltstones at various localities in the Lilydale area. The relative abundance of the species in the siltstones ranges between 6% and 100%, with assemblages comprising one to six species in which *W. lilydalensis* is moderately under-represented or over-represented (Fig. 4). In the siltstones of the Eden Park Formation in the Eden Park area *T. (R.) otisi* occurs in monospecific assemblages or dominates a low diversity assemblage also containing rare *Odontochile formosa*. In these beds *T. (R.) otisi* is preserved predominantly as isolated sclerites or partly articulated exoskeletons, many of which can be recognised as moult assemblages. The holotype is a complete exoskeleton with the cephalon displaced and lying underneath the thoracopygon. The ratio of articulated specimens is 25%, 5% being typical phacopid moult assemblages and less than 1% being fully articulated individuals. *T. (R.) otisi* also occurs in the overlying Clonbinane Sandstone Member, in medium grained sandstone and coquina bioclastic lags. At PL300, Clonbinane it is under-represented (relative abundance 17%) in a higher diversity assemblage also containing *Echidnops hollowayi*, *O. formosa*, *Dicranurus* sp. and an

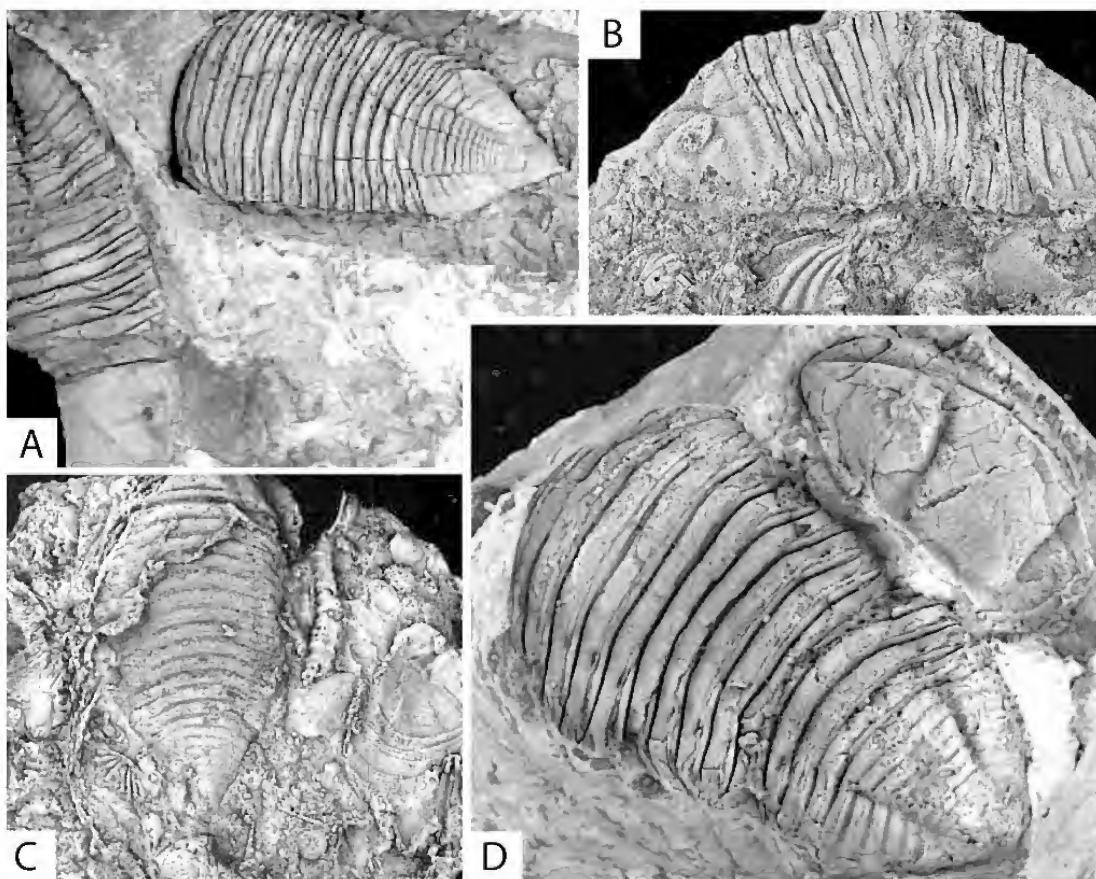


Figure 5 A, D. Moults assemblages of *Trimerus (Edgillia) kinglakensis* in the upper siltstones at PL252, Middendorps Quarry, Kinglake West, Humevale Siltstone. A, upper right, displaced and inverted cephalon lying underneath thoracopygon (only anterior margin visible); left, thoracopygon with displaced and rotated cephalon. D, thoracopygon with displaced and rotated cephalon. B–C. Complete dorsal exoskeletons in sandstone bioclastic coquinas. B, *Trimerus (Trimerus) harrisoni* from PL1820, Brunswick, Melbourne Formation. C, *Wendorfia lilydalensis* from PL1805, Coldstream. Humevale Siltstone.

odontopleurid. More than one third of all trilobites in these beds are complete, fully articulated exoskeletons. As in the bedded siltstones and coquina lags at Middendorps Quarry, the assemblage at PL300 is associated with a rich echinoderm fauna.

The taphonomy of the trilobite exoskeleton is an important palaeoenvironmental indicator. The multitude of sclerites of which the exoskeleton was composed responded in a complex way to the depositional environment in which they were ultimately preserved. Detailing the proportions of fragmented tergites, convex-up tergites, articulated tergites, enrolled individuals and moults assemblages in trilobite populations from the Middle Devonian Hamilton Group, New York, Speyer and Brett (1986) defined a sequence of trilobite taphofacies (taphofacies 1A–B, 2A–B, 3A–B and 4A–C) interpreted to reflect depth and rates of sedimentation. Sandford (2002)

described a similar depth-related sequence of trilobite taphofacies for the phacopid-dominated assemblages (TpI–TpIV) and the homalonotid-dominated assemblages (ThI–ThIV) of the Late Silurian–Early Devonian of south-eastern Australia. Whilst there is some credit in distinguishing between taphonomies for thick-shelled forms and thin-shelled forms in shallower facies, these forms occur in both phacopids and homalonotids. The separate Tp–Th classification of taphonomies is not justified, and abandoned here in place of a broader TI–IV classification, which can be more widely applied to trilobite taphofacies. Although this study is based almost entirely on museum specimens and the proportion of convex-up specimens cannot be accurately determined, Speyer and Brett's taphofacies can be recognised for the homalonotid faunas of south-eastern Australia. Assemblages preserved in fine-grained

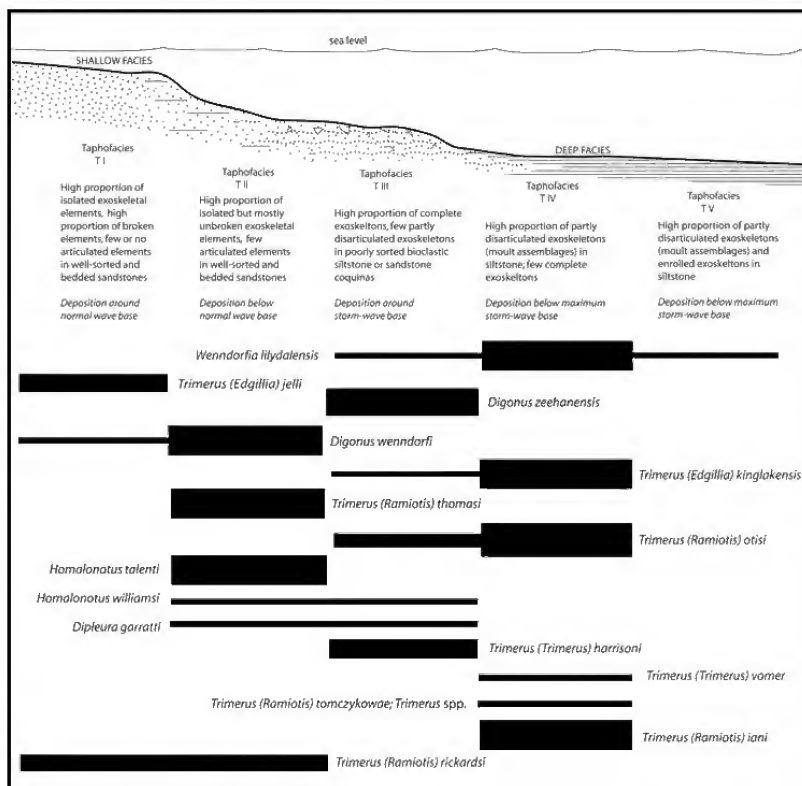


Figure 6. Facies and environmental distribution of Australian homalonotids.

lithologies with a high relative abundance of mould assemblages (or partly disarticulated exoskeletons), a low abundance or absence of complete, fully articulated exoskeletons, a low degree of isolated sclerites and low or negligible breakage can be assigned to Sandford's taphofacies TIV (~Speyer and Brett's taphofacies 4A). The preservation of mould assemblages indicates deposition at depths below maximum storm wave base, where current activity was minimal and reworking of exoskeletal elements was negligible. Assemblages preserved in poorly sorted bioclastic coquinal lags with a high relative abundance of complete, outstretched exoskeletons, an absence of mould assemblages and a moderate degree of breakage can be assigned to Sandford's taphofacies TIII. This taphofacies is interpreted to reflect depths around storm wave base and is analogous to Speyer and Brett's taphofacies 3A, although differing from it in the lower representation of mould assemblages and enrolled specimens relative to outstretched specimens. The basal lags represent proximal tempestites generated from the peak of storm activity, during which highest energy currents rapidly concentrated and buried large bioclasts (both living and dead), with complete exoskeletons representing smothered individuals.

Taphofacies associations for *Wenndorfia lilydalensis*, *Trimerus (Edgillia) kinglakensis* and *Trimerus (Ramiotis) otisi* populations demonstrate that the low diversity, homalonotid-dominated assemblages inhabited deeper bathymetries than the higher diversity assemblages in which homalonotids are under-represented. A similar relationship can be demonstrated for populations of *Digonus wenndorfi* from the Heathcote sequence, but in a shallower water context. At several localities including the type locality PL2204, Heathcote, *D. wenndorfi* occurs in abundance in monospecific or very low diversity assemblages. The taphonomy is characterised by a high relative abundance of isolated sclerites (80-95%), minimal breakage and a high concentration of elements, with the articulated specimens mostly represented by cephalia. Thick-bedded, medium to coarse-grained, well-sorted sandstone lithologies are associated with this taphofacies. Sandford (2002) designated this preservation taphofacies TII, equivalent to Speyer and Brett's (1986) taphofacies 1B, and it is interpreted to reflect deposition at depths around normal wave base, where moderate energy current action gently winnowed finer sediments, and disarticulated and concentrated skeletal elements in coarser lithologies. At PL2327, Heathcote *D. wenndorfi* occurs in a high diversity

fauna of ten species as a proportionally represented species (relative abundance 11%). The assemblage is dominated by *Echidnops hollowayi* and *Odontochile formosa*. In contrast to the preservation of the *D. wenndorfi*-dominated assemblages, that at PL2327 is characterised by a high proportion of isolated and broken sclerites (broken specimens 20%, isolated sclerites 98%). This preservation is generally associated with coarser-grained lithologies, typically thick, coquina sandstone with poorly sorted, randomly oriented bioclasts and can be assigned to Sandford's taphofacies TI, equivalent to Speyer and Brett's taphofacies 1A. A high proportion of isolated and broken sclerites suggests an environment of deposition in very shallow environments (<20 m) above normal wave base, with medium to high energy oscillatory wave-generated currents reworking, fragmenting and winnowing skeletal elements.

The paired assemblages occur variously in very shallow, moderate or deep water facies that reflect specific environmental tolerances and preclude the definition of discrete assemblage-facies associations. The facies distribution of south-eastern Australian homalonotids is shown in Fig. 6.

The relationship between homalonotid-dominated low diversity assemblages in deeper water facies and high diversity assemblages in which homalonotids are minor faunal elements in shallower-water facies are not generally consistent with Mikulic's (1999) and Thomas' (1979) observations that homalonotid species dominating shallow-water assemblages occur as rare elements of assemblages in deeper facies. For *Digonus wenndorfi*, *Trimerus* (*Edgillia*) *kinglakensis* and *Trimerus* (*Ramiothis*) *otisi* the opposite is true, being under-represented or rare in shallower environments and dominant in deeper environments. Rather than declining in abundance in even deeper environments, species are replaced by a different species. *T. (E.) kinglakensis* inhabits the deeper environments of the Lochkovian, whereas *T. (E.) jelli* and *D. wenndorfi* inhabit the contemporary shallow and very shallow environments. Similarly, *T. (R.) otisi* inhabits the deeper environments of the late Ludlow, whereas *T. (R.) thomasi* inhabits the contemporary shallow environments. An exception is the distribution of *W. lilydalensis*, which is consistent with both the pattern described above and with the observations of Mikulic and Thomas. As noted above, *W. wenndorfi* is rare in the shallower coquina sandstones at PL1804 and dominates many of the trilobite faunas in the deeper siltstones of the upper Humevale Siltstone at Lilydale. In the siltstones, the association of *Acastella frontosa* and *W. lilydalensis* alternates with another association of calymenids and/or phacopids, variously comprising *Sthenarocalymene angustior* (Chapman, 1915), *Nephranomma debrae*, *N. lynnae* and *Lochkovella longisulcata* (Shergold, 1968). The latter association is dominant in the deepest water facies, with taphonomies including enrolled individuals and often occurring with *Harpidella* sp. in abundance. At the few localities where the association of *A. frontosa* and *W. lilydalensis* occurs in these deepest water facies it is only in low abundance with the calymenid-phacopid associations dominant. These mixed faunas resemble the deeper water equivalents of Thomas' *Acaste-Trimerus* association, where *Calymene* becomes common.

Systematic palaeontology

The description of the homalonotid trilobites from central Victoria is based on collections in Museum Victoria (NMV), registered with prefix P. This collection includes specimens previously held by the Geological Survey of Victoria (previously registered with prefix GSV) and the University of Melbourne, Geology Department. Other specimens cited include those at the Geological Survey of New Zealand (NZGS) (registered with prefix AR) and at the Canterbury Museum, Christchurch, New Zealand (registered with prefix ZFc). Trilobite specimens are preserved in mudstones as internal and external moulds. Internal moulds were coated with colloidal graphite, latex peels have been made from external moulds, and all have been whitened with ammonium chloride for photography. Trilobite localities are registered with prefix PL in Museum Victoria. These include previously published fossil localities of Jutson (1908: pl. 3), Thomas (1940a, 1940b, 1941, 1956, 1960), Gill and Banks (1950), Gill (1940: fig. 1; 1945: fig. 2), Talent (1964: fig. 1), Williams (1964: fig. 2), Moore (1965: fig. 1), VandenBerg (1970), Garratt (1972, 1977), Jell and Holloway (1983: fig. 1), Holloway and Sandford (1993: fig. 1), Wall et al. (1995: fig. 1) Rickards and Sandford (1998: fig. 6) and Sandford (2000: fig. 7; 2002: fig. 1; 2003: text-fig. 1; 2004: fig. 1; 2005: figs 2-4). Trilobite localities in the Heathcote, Kilmore-Kinglake West, Springfield and Lilydale areas are shown in Figs 8, 11 and 23.

Terminology used in this study for the description of the trilobite exoskeleton (Fig. 7) generally follows current standard nomenclature reviewed by Whittington (1997) and Whittington and Kelly (1997). Terminology specific to the description of homalonotid trilobites has been introduced by Tomczykowa (1975), Wenndorf (1990) and Whittington (1993). Wenndorf established several new terms including 'Außendorn', referred to as the posterolateral pleural spine in this work, and the 'Gelenkleiste' in reference to ridges that overhang and partly enclose the trench-like furrow traversing each thoracic segment. Wenndorf also established a set of measurements and derived ratios specifically for the description of homalonotids. In accord with Wenndorf, the glabellar width is measured across L1-L1 rather than the across occipital ring (where the axial furrows are very poorly defined) and the pygidial axial width is measured across the second axial ring rather than the first ring, for the same reason. To avoid ambiguity this width is referred to as the preoccipital glabellar width. However in this work, following the description of other trilobites, the glabellar length includes the length of the occipital ring and the pygidial axial length includes the length of the terminal axial piece. Whittington (1993) introduced the term 'articulating and pleural furrow' to describe the furrow traversing thoracic segments, considered to be homologous to the independent pleural and articulating furrows of other trilobites. 'Rib-ring offset' is a term introduced in this work to describe differences in segmentation of the pygidial axis and pleural lobe in homalonotids. Rib-ring offset is a modification of R-P ratios often described for encrinurids, but impractical in describing homalonotid pygidia where segmentation is often poorly defined or effaced posteriorly. It is expressed by the n-th pleural rib when the transverse midline of that rib intersects with the axial furrow opposite a pygidial ring furrow.

Order PHACOPIDA Salter, 1864

Suborder CALYMENINA Swinnerton, 1915

Superfamily CALYMENOIDEA Burmeister, 1843

Family **Homalonotidae** Chapman, 1890

Remarks. Organisation of the Homalonotidae here follows Thomas (1977) who discussed previous divisions of the family.

Subfamily **Homalonotinae** Chapman, 1890

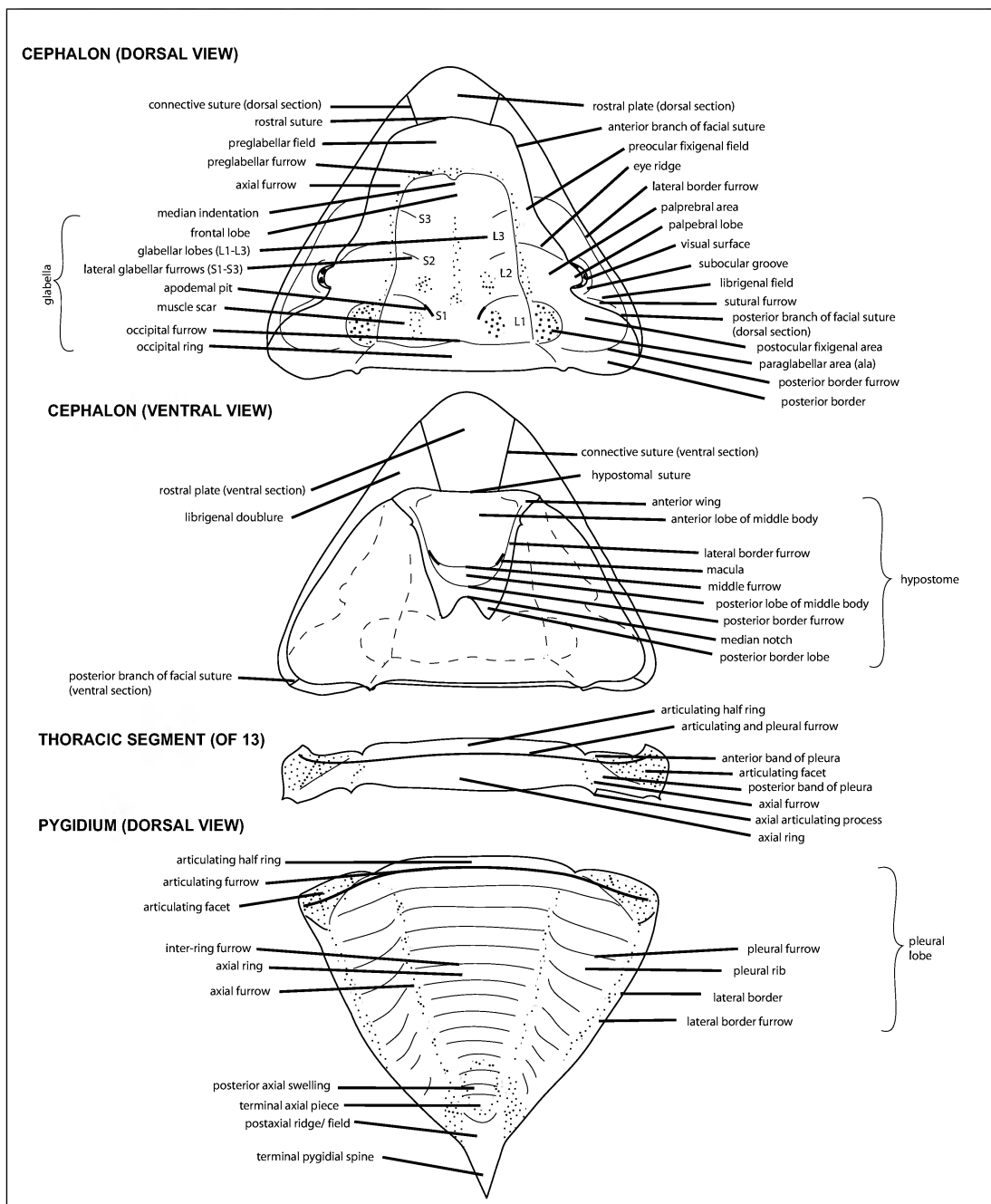


Figure 7. Morphological terms for the homalonotid exoskeleton.

Genera and subgenera included. *Homalonotus* König, 1825, *Trimerus* (*Trimerus*) Green, 1832, *Trimerus* (*Ramiotis*) subgen. nov., *Trimerus* (*Edgillia*) subgen. nov., *Digonus* Gürich, 1909, *Dipleura* Green, 1832, *Brongniartella* Reed, 1918, *Burmeisteria* Salter, 1865, *Burmeisterella* Reed, 1918, *Scabrella* Wenndorf, 1990, *Arduenella* Wenndorf, 1990, *Parahomalonotus* Reed, 1918, *Platycoryphe* Foerste, 1919, *Wenndorfia* gen. nov.

Discussion. Classifications of the Homalonotinae by Reed (1918), Sdzuy (1959), Tomczykowa (1975), Thomas (1977) and Wenndorf (1990) have variously emphasised particular features of the exoskeleton including glabellar lobation, glabellar outline, the course of the cephalic suture, the length of the preglabellar field, the morphology of the anterior cephalic margin, the shape of the rostral plate, the expression of a rostral process, eye position, pygidial outline, the outline of the pygidial axis, and the expression and degree of pygidial segmentation as characters of generic significance. Differences between these classifications reflect different emphases on diagnostic characters. The diversity of morphologies expressed within genera is greatly enhanced by the Australian fauna and necessitates a review of current generic concepts. A new genus *Wenndorfia* and two new subgenera *Trimerus* (*Ramiotis*) and *T.* (*Edgillia*) are described, and revised diagnoses are given for *Trimerus*, *Homalonotus*, *Dipleura*, *Digonus* and *Parahomalonotus*.

Homalonotus König, 1825

Homalonotus König, 1825:104.

Koenigia Salter, 1865: 119.

Type species. *Homalonotus knightii* König, 1825 from the Ludlow of England, by monotypy. The type species has been recorded from Britain, Germany, Poland and Canada, although its the relationship to the Canadian *H. dawsoni* is not clearly established. Hall (1860) described *dawsoni* solely from pygidia, and his diagnosis clearly allies the species with *knightii* and the Swedish *H. rhinotropis*. McLearn (1924) suggested that differences in pygidial morphology easily distinguish *dawsoni* from *knightii*, citing the posterior projection of the pygidial axis, narrower proportions and less convex profile of the lateral margin as distinguishing the type species. On these criteria McLearn identified specimens from the McAdam and Moydart Formations at Arasaig, Nova Scotia as *knightii*, and those from the slightly younger Stonehouse Formation in the same area as *dawsoni*. The cephalic morphology of *dawsoni* was described by Dawson (1868, 1877) and McLearn. McLearn noted that the two cephalia known from the McAdam and Moydart Formations were very similar to those of *dawsoni* from the Stonehouse Formation. Indeed, a relatively undeformed cephalon from the Moydart Formation examined by the author is clearly attributable to *dawsoni* rather than *knightii*. The specimen is comparable to the Stonehouse Formation cephalia in the anterior placement of the eyes and more elongate and more weakly tapering glabellar shape, distinguishing the Canadian species from the type species. The specimen also shows the acutely pointed lateral cusps of the anterior margin, not previously documented. Whether the differences in pygidial morphology between the McAdam and Moydart Formation populations are significant is a question that cannot be resolved without detailed re-examination of the faunas.

Other species included. *Homalonotus dawsoni* Hall, 1860, *H. rhinotropis* Angelin, 1852, *H. williamsi* sp. nov., *H. talenti* sp. nov.

Range. Ludlow, possibly early Pfäldorf. England, Germany, Poland, Sweden, eastern North America and south-eastern Australia.

Revised diagnosis. Cephalon much wider than long. Glabella long (length 1.1–1.3 times width), tapering forward weakly to moderately (15–30°), sides straight, lobation weak to indistinct. Paraglabellar area distinct. Preglabellar furrow present, of variable depth (shallow to very deeply impressed). Preglabellar field very short (<0.08 times cranial length). Anterior margin of cephalon tricuspid with a strongly folded (M-shaped) profile in dorsal view. Central cusp triangular, and strongly convex downwards in anterior view. Facial suture and rostral suture meeting at invagination of anterior margin such that connective suture is absent dorsally. Eyes forwardly placed, opposite 0.55–0.7 glabellar length. Pygidial lateral border furrow distinct, anteriorly lateral border swollen, lip-like, fused ventrally with rolled doublure and continuous with long (exsag.) articulating facet.

Discussion. Sdzuy's (1959) diagnosis of *Homalonotus* reiterates the characters listed by Reed (1918), omitting only the 'angular course of the anterior branch of the facial suture'. Additional characters listed by Sdzuy include features of the glabella (indistinct lobation, trapezoidal shape), the rostral plate (lacking a process), the folding of the anterior margin, and the presence of a cephalic border (i.e. that defined by the preglabellar furrow). The preglabellar furrow is variable in depth, being very deeply impressed in *H. williamsi* and *H. talenti*, moderately impressed in *H. dawsoni* (see McLearn, 1924: pl. 27, fig. 14) and *H. rhinotropis* (see Angelin, 1878: pl. 20, fig. 1). In the type species, the depth of the preglabellar furrow varies from shallow (e.g. Tomczykowa, 1975: pl. 1, figs 1, 3) to moderately impressed (e.g. Salter, 1865: pl. 12, fig. 2) and suggests the presence/absence rather than the depth of the furrow is of significance.

The assignment of two new Australian species to the genus indicates a somewhat broader range of morphologies for the genus than represented by the northern hemisphere species, particularly in features of the pygidium. *Homalonotus knightii*, *H. rhinotropis* and *H. dawsoni* share a distinct pygidial morphology characterised by raised, long pleural ribs that are continuous with the axial rings (separated by a deep, continuous, pleural and ring furrows), effaced axial furrows, by a fused postaxial ridge and posterior area of pleural field, and by a strongly acuminate tip. In contrast, the pygidial axial furrows of *H. williamsi* and *H. talenti* are only moderately impressed (Figs 10.3–10.11). In *williamsi* the axis is raised, defining distinct pygidial trilobation, the postaxial ridge is not fused with the posterior area of the pleural field, whilst in *talenti* the pleural and ring furrows are shallow and the posterior tip is rounded. The revised diagnosis given above accommodates these morphologies by excluding all pygidial characters listed in Sdzuy's (1959) and Tomczykowa's (1975) diagnoses, including the 'acuminate triangular and acutely tipped pygidial outline', the 'weakly defined trilobation', the 'posterior fusion of axis and pleural field' and the 'distinct segmentation'. Nevertheless, the pygidial morphology characterising the contemporary northern-hemisphere species defines a species group distinct from the Australian taxa and reflects a degree of provincialism not otherwise seen in homalonotid distribution.

The distinctive morphology of the pygidial lateral border is

listed as an additional diagnostic character. The complex anterior cephalic margin of *Homalonotus* corresponds to a complex coaptive morphology. Laterally, the swollen, lip-like section of the pygidial border-doublure defines the overlap of the librigena, the pygidial border-doublure fitting against the cephalic doublure. The pygidial doublure is narrow posterior to the lip-like section, and at this point the doublure of the enrolled pygidium emerged from underneath the anterior cephalic border at the invagination of the anterior margin. The anterior margin of the rostral process fitted against the posterior margin of the pygidial doublure, as indicated by the matching convexity of these structures (in anterior/posterior view) in *H. talenti* (Figs 9.5b, 10.7c).

Several of the cephalic features listed as generic characters by Sdzuy (1959) are excluded from the revised diagnosis, including the 'indistinct glabellar lobation' and the 'median point on the rostral suture'. These characters are excluded to accommodate the Australian species, that lack a median point on the rostral suture, whilst *Homalonotus williamsi* exhibits weak glabellar lobation. Sdzuy noted the difficulty in interpreting the anterior border of *Homalonotus*. However, the junction of the facial suture and rostral suture at the invagination of the anterior margin (and the absence of the connective suture dorsally) is clearly evident on *williamsi*, and is comparable to the morphology of the anterior margin of *H. rhinotropis* described by Moberg and Grönwall (1909).

Sdzuy (1957), Tomczykowa (1975) and Thomas (1977) considered *Homalonotus* to have been derived from *Trimerus* and interpreted *H. (T.) johannis* Salter, 1865 as transitional between the genera. Wenndorf (1990) expressed uncertainty on this derivation of *Homalonotus*. Reed (1918) tentatively placed *johannis* in *Homalonotus*, primarily on account of its tricuspid, folded anterior margin and supposed pygidial similarities, but noted that long preglabellar field of *johannis* differed markedly from that of *H. knightii*. Although Prantl and Přibyl (1948) suggested a new genus or subgenus be erected for *johannis*, Sdzuy (1957) retained the species in *Homalonotus*. The length of the preglabellar field is only one of many differences between *knightii* and *johannis* indicating that these species are not related. Whilst *johannis* shares with the northern hemisphere species of *Homalonotus* (*knightii*, *H. dawsoni* and *H. rhinotropis*) deeply impressed pygidial pleural and ring furrows and an elongate, acutely tipped triangular outline, it lacks the effaced trilobation and fused postaxial area characterising those species. More importantly, *johannis* lacks the swollen lip-like pygidial border shared also by the Australian species and considered diagnostic of the genus. The species also differs markedly from *Homalonotus* in having a highly derived cranidial morphology. The raised glabella which is markedly expanded across L1-L1 (tr.) and has deep S1 apodemes and a distinct sagittal ridge, the strong expression of the medial indentation of the anterior glabellar margin and paraglabellar areas, and the long and weakly convex (tr.) preglabellar field indicates assignment of Salter's species to *Trimerus* (*Trimerus*), in agreement with Tomczykowa's (1975) and Morris' (1988) assignment.

Of the species assigned in this work to *Homalonotus*, *H. williamsi* appears to be the least derived. *H. williamsi* retains

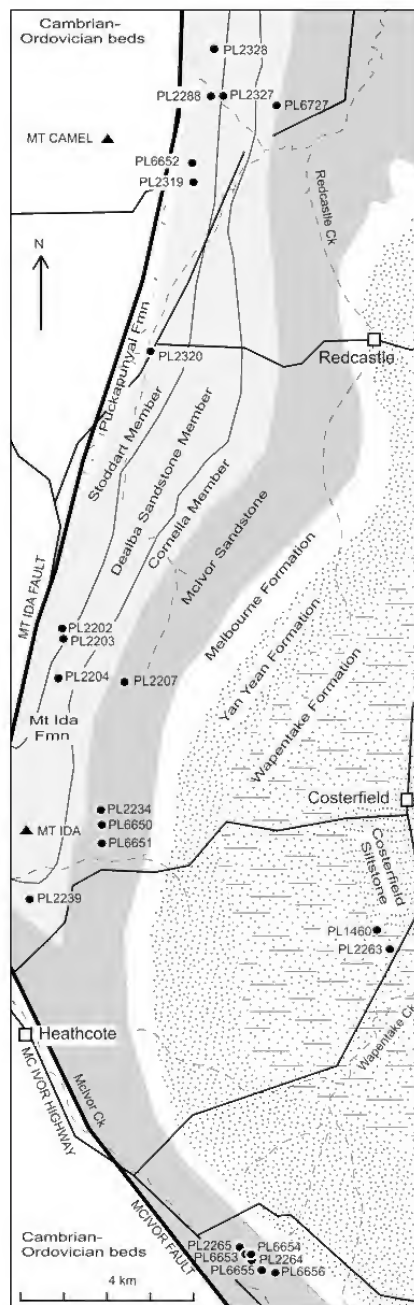


Figure 8. Geological sketch map of the Heathcote area showing Wenlock-Lochkovian fossil localities yielding homalonotids. For other fossil localities see also Thomas (1940a, 1940b, 1941, 1956), Talent (1964, fig. 1), Sandford (2002, fig. 1A; 2005, fig. 4).

distinct glabellar lobation, the axial furrows are moderately impressed, the pygidial axis is raised posteriorly and the postaxial area is not fused with the pleural field. In these respects *williamsi* shares features of *Trimerus* possibly reflecting the relationship suggested by Sdzuy, Tomczykowa and Thomas. The interpretation of *williamsi* as morphologically primitive supports the derivation of *Homalonotus* from *T. (Ramiotis)* rather than from the more derived *T. (Trimerus)*. Of species assigned to *T. (Ramiotis)*, *williamsi* bears closest resemblance to *T. (R.) otisi* (Fig. 20), which bears a well-developed tricuspid cephalic margin comparable to that of *T. (T.) johannis*, though more weakly folded. As with several other Upper Silurian species of *T. (Ramiotis)*, *otisi* also exhibits a well defined pygidial border furrow and swollen lip-like border comparable to that of *Homalonotus*, a morphology otherwise only poorly developed or absent in other groups including *T. (Trimerus)* and *T. (Edgillia)*. *T. (R.) otisi* lacks the strongly derived glabellar features of *johannis*, sharing with *Homalonotus* the elongated, weakly tapering glabella with weak lobation. In these respects *otisi* is a more likely candidate than *johannis* in representing an intermediate morphology between *Trimerus* and *Homalonotus*, although its interpretation as an ancestral species is not in accord with its stratigraphic position, *otisi* appearing in strata immediately overlying those yielding *williamsi*.

Homalonotus talenti sp. nov.

Figures 9, 10.5–10.11

Homalonotinae gen. et sp. indet. 2.—Holloway and Neil, 1982: 146, fig. 4I–L. — Morzadec, 1986: 186.

Type material. Holotype NMV P304936 (cephalon) from PL6650, Heathcote, Victoria (Fig. 9.1). Paratypes NMV P304927, NMV P304937–P304939 (cephala), NMV P304923–P304925, NMV P304928, P304929 (cranidia), NMV P304941, NMV P304943 (librigena), NMV P304946–P304948 (hypostomes), NMV P304945, NMV P304949 (thoracic segments), NMV P304917, P304918, NMV P304920–P304922 (pygidia) from PL6650. Paratypes NMV P304952, P304953 (pygidia) from PL6651, Heathcote. For localities see Fig. 8.

Previously figured material. NMV P78296 (ex GSV35724, cephalon, figured Holloway and Neil, 1982: figs 4I, 4J), NMV P78297 (ex GSV35725, pygidium, figured Holloway and Neil, 1982: figs 4K, 4L) from PL2239, Thomas locality F25, Parish of Heathcote, Heathcote. For locality see Fig. 8.

Registered material. 127 specimens: 10 cephalae, 41 cranidia, 9 librigenae, 3 hypostomes, 8 thoracic segments, 56 pygidia. NMV

P304917–P304951, NMV P304959–305026 from PL6650. NMV P304952–P304957, NMV P305027–P305029 from PL6651. NMV P304958, NMV P305041 from PL2265, Thomas locality F46, Parish of Heathcote, Heathcote. NMV P78296, P78297 from PL2239. NMV P305030–P305040 from PL2207, Thomas locality F7, Parish of Dargile, Heathcote. For localities see Fig. 8.

Stratigraphic distribution. Upper beds of the McIvor Sandstone and lowermost beds of the Cornella Member of the Mt Ida Formation, *Notoparmella plentiensis* Assemblage Zone, late Ludlow. The age of the McIvor Sandstone is constrained by early Ludlow (upper *nilsoni* Biozone) graptolite assemblages from the underlying Melbourne Formation (Rickards and Sandford, 1998). In Europe, *Homalonotus* occurs in abundance in strata of Ludfordian age, occurring rarely in the Gorstian (Thomas et al., 1989) and possibly ranging into the Přídolí. The first appearance of *H. talenti* about 380 m above the base of the McIvor Sandstone (at PL2265) is considered here to approximate the Gorstian-Ludfordian boundary. The Ludlow-Přídolí boundary can be placed within the interval between the last appearance of *talenti* (at PL2239) and the first appearance of the post-Ludlow brachiopod *Cyrtina* at a slightly higher horizon, 50–100 m above the base of Cornella Member.

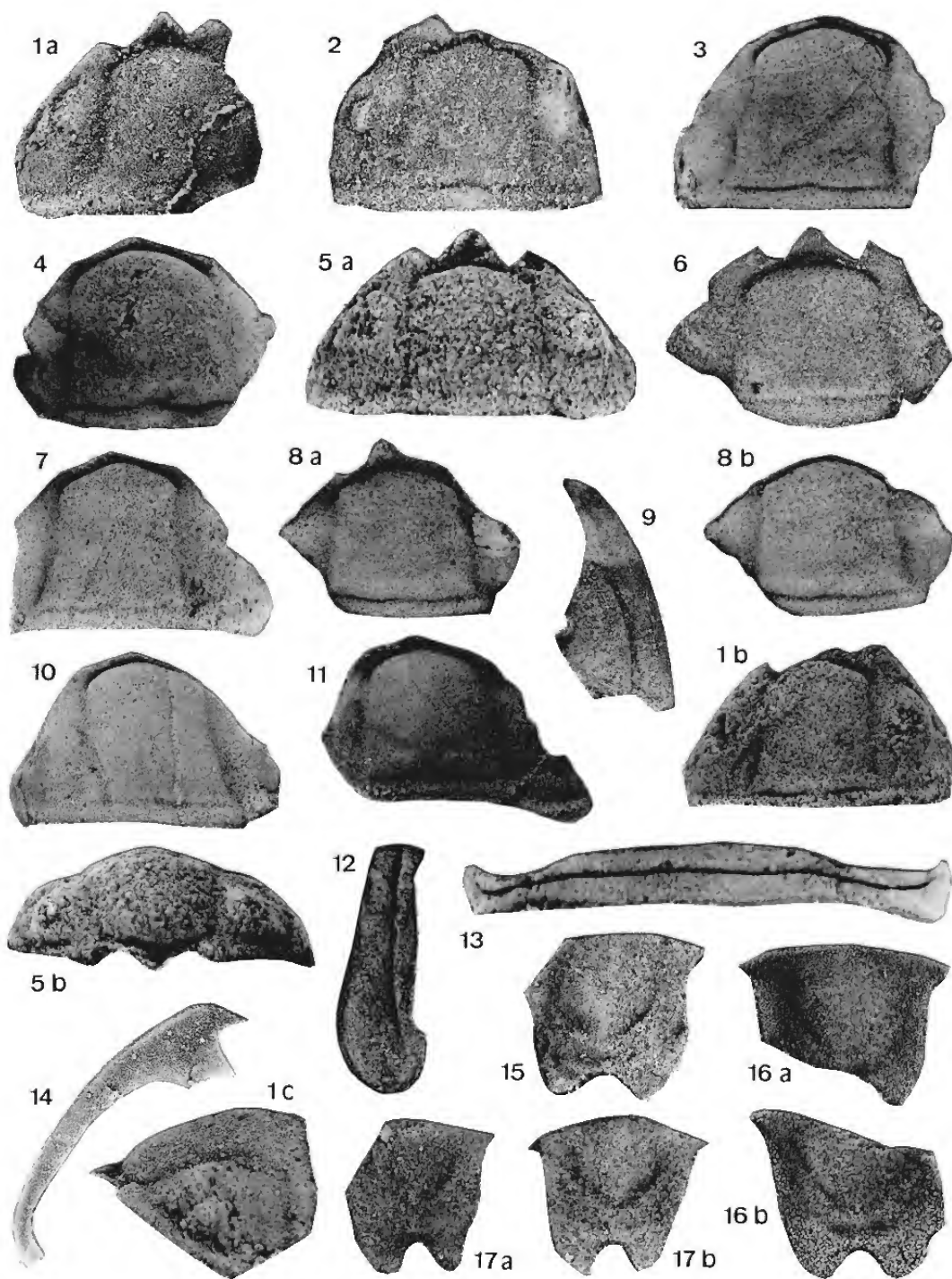
Derivation of name. For John A. Talent (Macquarie University), for his contribution to Victorian palaeontology.

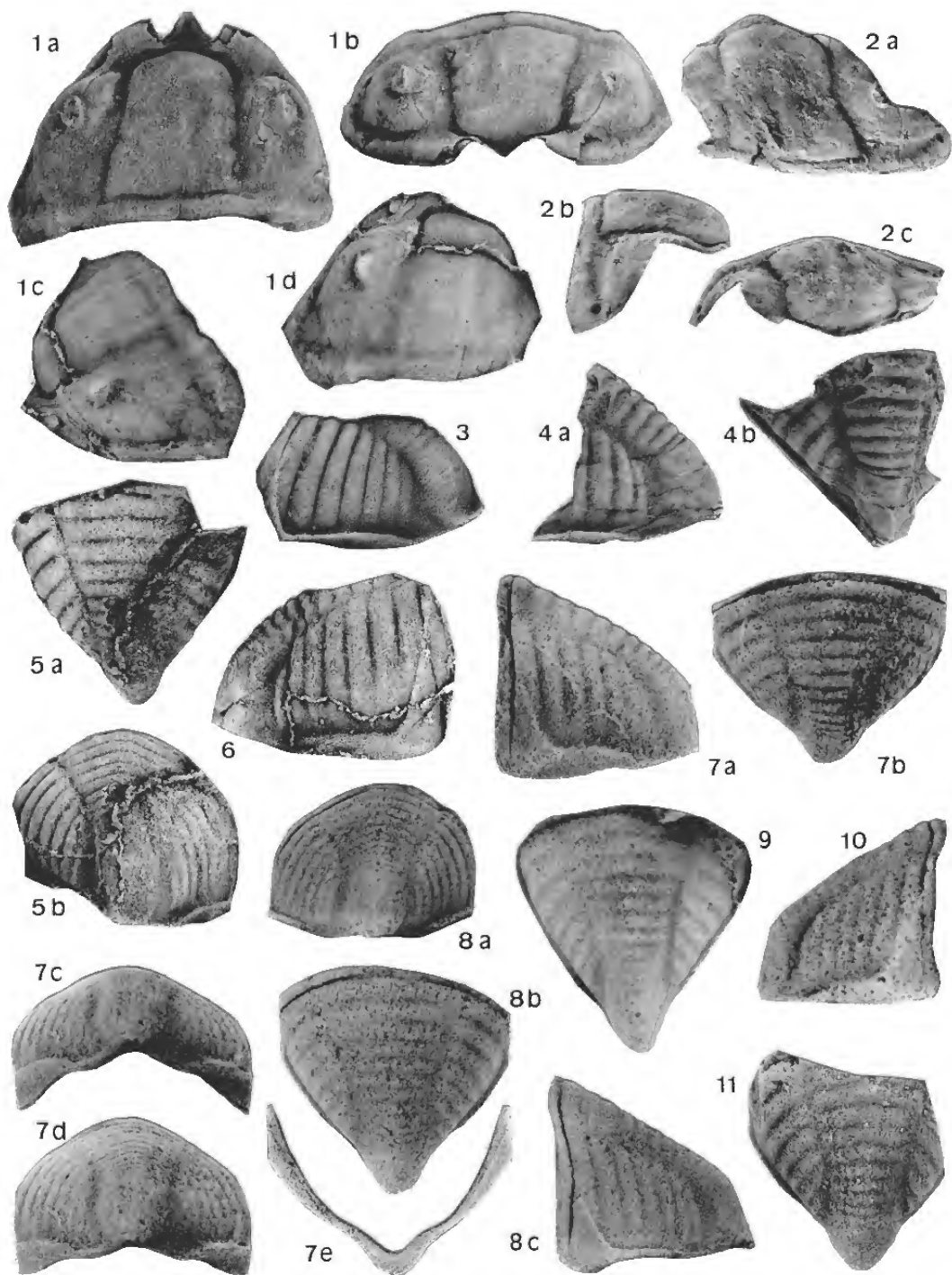
Diagnosis. Glabella trapezoid, sides straight and converging at 20°, anterior margin broadly rounded. Glabellar length about 1.1 times preoccipital glabellar width and 0.94 times cranial length. Preglabellar furrow very deeply impressed. Eye placed with midline of palpebral lobe opposite 0.56 glabellar length/0.52 cranial length. Dorsal surface of rostral plate 0.14 times cephalic length. Hypostome with length 0.85 width, lobes on the posterior border with length 0.17 times hypostomal length. Pygidium with length about 0.9 times width, postaxial ridge projecting posteriorly, tip rounded. Pygidial axis with width 0.5 times pygidial width, 11 axial rings. Axial furrows straight and tapering at about 30°. 7 pleural ribs, rib-ring medially offset at fourth rib. Ring, pleural and axial furrows shallow to moderately impressed.

Description. Exoskeleton of moderate size, maximum length estimated 12 cm (from NMV P305923), occipital convexity (tr.) moderate, pygidial convexity (tr.) strong.

Cephalon wide, length 0.6 times width, with trapezoid outline, sides moderately convex and converging forwards at about 75°, anterior margin tricusate, median cusp triangular in outline with rounded tip, length about 0.6 times width, lateral cusps with obtusely angled tips reaching forward to midlength of median cusp. Cranial width 1.9

Figure 9. *Homalonotus talenti* sp. nov. 1a, holotype NMV P304936, cephalon, dorsal view x 3.0 (latex cast) from PL6650. 1b, same, x 2.6 (internal mould). 1c, same, lateral view x 3.0 (latex cast). 2, paratype NMV P304938, cephalon, dorsal view x 2.6 (latex cast) from PL6650. 3, paratype NMV P304929, cranidium, dorsal view x 2.1 (internal mould) from PL6650. 4, paratype NMV P304923, cranidium, dorsal view x 1.65 (internal mould) from PL6650. 5a, paratype NMV P304927, cephalon, dorsal view x 5.5 (internal mould) from PL6650. 5b, same, anterior view x 5.0. 6, paratype NMV P304937, cephalon, dorsal view x 1.9 (latex cast) from PL6650. 7, paratype NMV P304924, cranidium, dorsal view x 3.6 (internal mould) from PL6650. 8a, paratype NMV P304939, cephalon, dorsal view x 2.0 (internal mould) from PL6650. 8b, same, x 2.1 (latex cast). 9, paratype NMV P304943, librigena, dorsolateral view x 1.22 (latex cast) from PL6650. 10, paratype NMV P304925, cranidium, dorsal view x 1.75 (internal mould) from PL6650. 11, paratype NMV P304928, cranidium, dorsal view x 1.6 (internal mould) from PL6650. 12, paratype NMV P304949, thoracic segment, lateral view x 1.75 (internal mould) from PL6650. 13, paratype NMV P304945, thoracic segment, dorsal view x 1.4 (internal mould) from PL6650. 14, paratype NMV P304941, librigenal doublure, ventral view x 2.4 (latex cast) from PL6650. 15, paratype NMV P304947, hypostome, ventral view x 2.2 (internal mould) from PL6650. 16a, paratype NMV P304946, hypostome, ventral view x 3.4 (latex cast) from PL6650. 16b, same (internal mould). 17a, paratype NMV P304948, hypostome, ventral view x 3.5 (internal mould) from PL6650. 17b, same (latex cast).





times length. Glabella with anterior margin strongly defined, arc of curvature centred at about glabellar midlength. Occipital ring about 0.1 times cranial length, slightly wider medially. Occipital furrow moderately impressed to shallow, with weak forward flexure medially. Glabellar lobation extremely weak (best seen on NMV P304928) to indistinct. L1 0.32 times glabellar length, L2 0.12 times glabellar length, L3 0.10 times glabellar length and frontal lobe 0.20 times glabellar length. S1 weakly convex, directed diagonally abaxially. S2 and S3 transverse. Axial furrows shallow to moderately impressed. Paraglabellar area very weakly defined. Length (sag.) of preglabellar furrow and ridge-like preglabellar field 0.03 times cranial length. Length (exsag.) of posterior border equal to occipital length adaxially, lengthening slightly abaxially. Posterior border furrow transverse, very wide and shallow, meeting lateral border furrow distally. Postocular fixigenal area long, length (exsag.) 0.25 times cranial length. Palpebral lobes placed anteriorly and remotely (δ - δ 1.5 times preoccipital glabellar width). Palpebral lobe length (exsag.) 0.15 times cranial length, palpebral furrow indistinct. Preocular fixigenal area of moderate width, width 0.17 δ - δ adjacent to palpebral area, eye ridges not distinct, narrowing markedly anteriorly. Anterior branches of facial suture converging at about 80°, curving inwards opposite the antero-lateral corner of the glabella and converging at about 140° anteriorly. Librigena with wide, moderately impressed border furrow, not continuing forward of antero-lateral corner of glabella, librigenal field weakly convex, steeply inclined, lateral border wide, convex. Anterior margin of librigena projecting far forwards from juncture of rostral, connective and facial sutures at cephalic margin as triangular cusp.

Course of rostral suture broadly rounded, concentric to anterior margin of glabella. Dorsal surface of rostral plate rounded triangular, length (sag.) 0.4 times width, strongly concave (tr. sect.). On cephalic doublure connective sutures straight and weakly converging posteriorly. Librigenal doublure without distinct vincular furrow, strongly convex (exsag. sect.) adjacent to connective suture (i.e. accommodating preglabellar furrow). Hypostomal suture very broadly rounded.

Hypostome with middle furrow shallow to moderately impressed, anterior wing process small (width 0.1 times hypostomal width), lobes on posterior border parabolic in outline, deep medial notch with sides converging at about 75°.

Thorax with axial furrows poorly defined. Pleural furrows narrow (exsag.) and deep, pleural tips rounded.

Pygidium with triangular outline, sides weakly convex and converging at about 80°. In lateral view pygidium high, height equal to length. Pygidial axis reaching to about 0.8 times pygidial length, continuous posteriorly with wide postaxial ridge. Postaxial ridge raised, parallel-sided, wide, width (tr.) 0.45 times axial width, posterior margin with parabolic outline. Axial furrows tapering, curving to the exsagittal posteriorly, shallow anteriorly, moderately impressed posteriorly. Pleural furrows shallowing markedly adjacent to border furrow. Border furrow moderately impressed opposite pleural field, shallow opposite postaxial ridge. In dorsal view border narrow (tr.) but pro-

tuberant from margin of pleural field. In lateral view border very wide anteriorly, merging with wide articulating facet, narrowing markedly posteriorly. Lateral border continuous with narrow pygidial doublure. In posterior view anterior margin of pygidium strongly convex, posterior margin with distinct medial and lateral arches. In ventral view, inner margin of doublure parabolic in outline with deep medial indentation.

Dorsal exoskeleton finely granulose. Pygidial border with fine ridging.

Discussion. Holloway and Neil (1982) suggested the affinities of an incomplete cephalon examined by them were with *Homalonotus*. Their suggestion is confirmed with the additional specimens listed. They noted similarities between the associated pygidium and that of the South American Lower Devonian species *H. clarkei*, but these similarities are superficial. Following Cooper (1982), and as discussed below, *clarkei* is assigned to *Burmeisteria*.

Hypostomes are also known for *Homalonotus knightii* and *H. rhinotropis* (Salter, 1865: pl. 12 fig. 10; Angelin, 1878: pl. 20 fig. 1c). The hypostome of *H. talenti* most closely resembles that of the type species. The hypostome of *rhinotropis* is relatively elongate (length times 1.1 width) compared to that of *knightii* (length 0.81 times width) and *talenti* (length 0.85 times width). The projections of the posterior margin are broadly based and long in *talenti* and *knightii*, but short in *rhinotropis*.

Although the ventral surface of the rostral plate of *Homalonotus talenti* is not known, the course of the connective sutures (indicated by the shape of the librigenae) is more or less straight and slightly convergent posteriorly, indicating the rostral plate to be approximately pentagonal, with subequal sides. Apparent curvature of the connective sutures on Fig. 9.14 is due to the oblique orientation of the specimen.

The broad, rounded medial indentation of the inner margin of the pygidial doublure of *Homalonotus talenti* (Fig. 10.7e) differs from that of *H. knightii*, in which the margin is more or less straight laterally, and defines an acute angle medially (see Salter, 1865: pl. 12 fig. 9a, Tomczykowa, 1975: pl. 1 fig. 5c).

Environmental notes. Throughout its range *Homalonotus talenti* occurs in thick-bedded fine- to medium-grained sandstones, in low diversity or monospecific assemblages. At the type locality where the species occurs in greatest abundance the proportion of articulated specimens is low (6%) and the proportion of broken specimens low (3%). The fauna can be assigned to taphofacies TII and indicates shallow environments around normal wave base.

Homalonotus williamsi sp. nov.

Figures 10.1–10.4

Type material. Holotype NMV P308674 (cephalon) from PL6615, Jutson locality VII, Eden Park, Victoria (Fig. 10.1). Paratypes NMV P308675 (pygidium), NMV P308676 (cephalon) from PL6615. Paratype NMV P304511 (pygidium) from PL6614, Jutson locality VI, Eden Park. For localities see Fig. 11.

Figure 10.1–10.4 *Homalonotus williamsi* sp. nov. 1a, holotype NMV P308674, cephalon, dorsal view $\times 2.1$ (internal mould) from PL6615. 1b, same, anterior view. 1c, same, oblique view $\times 2.3$ (latex cast). 1d, same, dorsal view. 2a, paratype NMV P308676, cranium, dorsal view $\times 1.3$ (internal mould) from PL6615. 2b, same, lateral view $\times 1.2$. 2c, same, anterior view $\times 1.3$. 3, paratype NMV P308675, pygidium, oblique view $\times 3.0$ (latex cast) from PL6615. 4a, paratype NMV P304511, pygidium, oblique view $\times 1.35$ (internal mould) from PL6614. 4b, same, dorsal view $\times 1.45$.

Figure 10.5–10.11, *Homalonotus talenti* sp. nov. 5a, paratype NMV P304952, pygidium, dorsal view $\times 1.1$ (latex cast) from PL6651. 5b, same, posterodorsal view. 6, paratype NMV P304953, pygidium, oblique view $\times 1.2$ (latex cast) from PL6651. 7a, paratype NMV P304921, pygidium, lateral view $\times 1.6$ (internal mould) from PL6650. 7b, same, dorsal view. 7c, same, posteroventral view. 7d, same, posterior view. 7e, same, ventral view (doublure). 8a, paratype NMV P304917, pygidium, posteroventral view $\times 1.2$ (internal mould) from PL6650. 8b, same, dorsal view $\times 1.6$. 8c, same, lateral view $\times 1.4$. 9, paratype NMV P304918, pygidium, dorsal view $\times 2.6$ (latex cast) from PL6650. 10, paratype NMV P304920, pygidium, lateral view $\times 2.7$ (internal mould) from PL6650. 11, paratype P304922, pygidium, dorsal view $\times 1.5$ (internal mould) from PL6650.

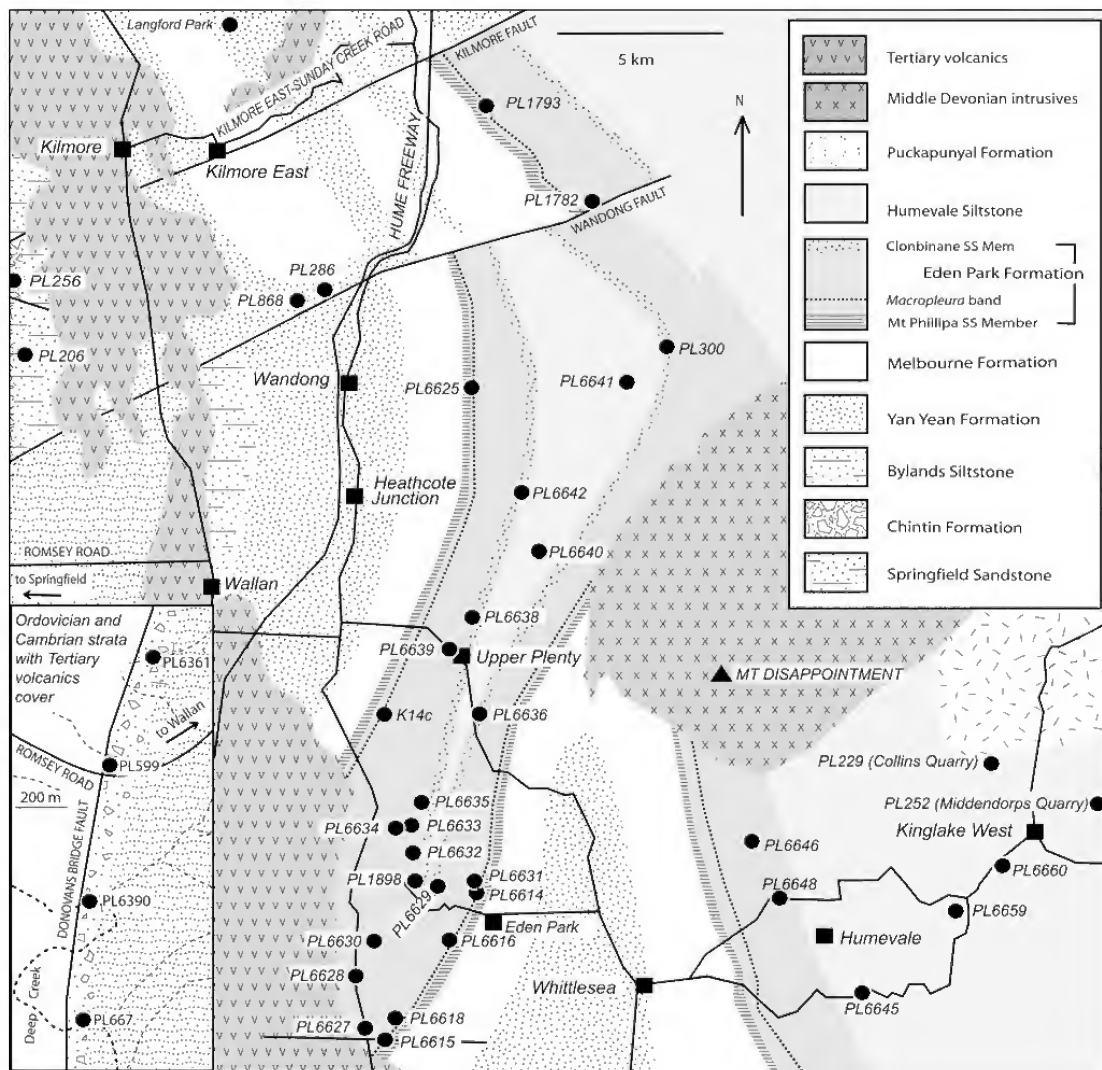


Figure 11. Geological sketch map of the Springfield-Kinglake West area showing Llandovery-Lochkovian fossil localities yielding homalonotids. For other fossil localities see also Jutson (1908, pl. 3), Thomas (1960), Talent (1964, fig. 1), Williams (1964, fig. 2), Garratt (1972, 1977), Rickards and Sandford (1998, fig. 6), Sandford (2002, fig. 1C; 2005, figs 2–3).

Other material. NMV P304512 from PL6614.

Stratigraphic distribution. *Macrolepura* band, Eden Park Formation (130–140 metres above base of unit), lowermost *Notoparmella plentiensis* Assemblage Zone, early-mid Ludlow.

Derivation of name. For George E. Williams, for his contribution to Victorian stratigraphy.

Diagnosis. Cephalon wide, length 0.6 times width. Glabella long, length 1.15 times width, sides more or less straight, taper-

ing at about 15°, anterior margin broadly rounded, arc centred at 0.55 glabellar length. Glabellar length 0.92 times cranial length. Glabellar lobation distinct, S1 and S2 expressed as deep notches adjacent to the axial furrows but very shallow abaxially, placed opposite 0.43 and 0.63 glabellar length respectively. Axial furrows moderately impressed on internal moulds (shallow on external moulds), preglabellar furrow very deeply impressed. Rostral plate with length of dorsal surface 0.11 times cephalic length, width (across rostral suture) 1.9 times

length, triangular. Genae moderately swollen, lateral border furrow moderately impressed. Eye placed with midline of palpebral lobe opposite 0.67 glabellar length. Anterior branch of facial suture with posterior section straight and strongly convergent (at about 90°), anterior section evenly curving to the transverse. Rostral suture weakly convex. Pygidium triangular in outline, sides straight, converging posteriorly at about 100°. Axial furrows moderately impressed. Pygidial axis strongly convex, raised, sides converging at about 25°, continuous posteriorly with wide postaxial ridge. Pleural field with 7 ribs. Pleural and ring furrows moderately impressed, of subequal depth.

Discussion. *Homalonotus williamsi* closely resembles *H. talenti* from the lower Ludlow-lower Přídolí strata of the Heathcote area. Differences in cephalic morphology are subtle, but *talenti* can be distinguished in that the glabella is less elongate (glabellar length 1.1 times width) S1-S3 are extremely weakly impressed to indistinct, the axial furrows are much shallower, the preglabellar furrow and preglabellar field are notably shorter (exsag. and sag., glabellar length 0.95 times cranial length), the eyes are more posteriorly placed (midline of palpebral lobe opposite 0.55 glabellar length), and the rostral process is wider posteriorly and only weakly convex downwards. The pygidium of *williamsi* is known only from fragments, but differs from that of *talenti* in having deeper axial, ring and pleural furrows.

In addition to the pygidial characters and the very deep, trench-like preglabellar furrows distinguishing the two Australian species from the northern-hemisphere species, *Homalonotus talenti* and *H. williamsi* also share straight and strongly convergent anterior branches of the facial sutures, in contrast to the convex outwards course of the sutures in *H. knightii*, *H. dawsoni* and *H. rhinotropis*. The Australian species and *rhinotropis* share a rounded anterior glabellar margin, differing from the transverse margin of *knightii* and *dawsoni*.

Environmental notes. See *Dipleura garratti* sp. nov.

***Brongniartella* Reed, 1918**

Type species. *Homalonotus bisulcatus* Salter, 1851 from the Upper Ordovician of England, by original designation.

***Brongniartella* sp.**

Trimerus sp.—Holloway and Sandford, 1993: 93, fig. 4L, non figs 4C-D, 4F-G, 4I-J, 4N-P.

Material. NMV P137228 (pygidium, figured Holloway and Sandford, 1993: fig. 4L) from PL359, Tiger Range, northwest of Maydena, Tasmania. For locality see Holloway and Sandford: fig. 1.

Stratigraphic distribution. Richea Siltstone, *Monograptus griestoniensis*-*M. crenulata* biozones, upper Llandovery.

Notes. The elongate, rounded parabolic outline of the pygidium, the strongly raised, narrow, convex pygidial axis and the indication of a distinct border suggest assignment to *Brongniartella*. The concave sides of the axis is shared with other species of *Brongniartella*. The species is a late appearance for *Brongniartella*, a predominantly Upper Ordovician

genus but known to extend into the Lower Llandovery *atavus-cyphus*? biozones in Britain (Temple, 1975) and also recorded from the Lower Llandovery of Jordan (Wolfart et al., 1968). The Upper Llandovery Tasmanian record narrows the gap between Lower Llandovery *Brongniartella* and the youngest known species, *B. pamiricus* (Balashova, 1966) from the Wenlock of Pamir, central Asia.

***Digonus* Gürich, 1909**

Type species. *Homalonotus gigas* Roemer, 1843, from the Lower Devonian (Emsian) Kahleberg Sandstone, Germany, by original designation.

Other species and subspecies included. *Burmeisteria* (*Digonus*) *antarcticus* Saul, 1965, *D. armoricanus* Pillet, 1961a, *D. asturco* Kegel, 1927, *Homalonotus crassicauda* Sandberger and Sandberger, 1849, *D. gigas posterior* Wenndorf, 1990, *H. goniopygaeus* Woodward, 1882, *H. (D.) harpyius* Richter and Richter, 1932, *H. intermedius* Vietor, 1919, *H. laticaudatus* Williams and Breger, 1916, *H. (D.) ornatus disornatus* Richter and Richter, 1932, *D. ornatus linguatus* Wenndorf, 1990, *H. ornatus* Koch, 1883a, *D. comes* Chlupáč, 1981, *H. roemeri* de Koninck, 1876, *D. wenndorfi* sp. nov., *Trimerus zeehanensis* Gill, 1949, *D. zemmourensis* Pillet, 1961b, *Digonus* sp. A in Wenndorf (1990).

Other species tentatively included. *Digonus collini* Renaud, 1942, *Homalonotus derbyi* Clarke, 1890.

Range. Lochkovian-Emsian.

Diagnosis. Cranium trapezoidal in outline, anterior margin with median cusp. Dorsal section of connective sutures very short. Glabella trapezoidal in outline, sides straight or very weakly concave. Glabellar lobation very weak or absent. Paraglabellar area distinct. Anterior outline of cranium quadrate, anterior branches of facial suture more or less straight between palpebral lobe and midlength of preglabellar field and converging at an acute angle (20–60°), curving abruptly to the transverse anteriorly. Rostral suture transverse to weakly concave. Ventral surface of rostral plate with thorn, spine or keel. Pygidium triangular to elongate triangular, with wide axis (0.5–0.7 times pygidial width). Axis with weak independent convexity (tr. sect.), postaxial ridge not raised. Pleural and ring furrows deep to very deep, more or less equal in depth. Axial furrow shallow or moderately impressed posteriorly, very shallow or effaced anteriorly, anteriormost ribs and rings fused, with corresponding section of axial furrow effaced or reduced to shallow invagination in posterior margin of segment. Pleural furrows maintaining uniform depth to a point close to border. Border furrow and border poorly defined. Rib-ring offset high (fifth–seventh rib).

Discussion. Previous diagnoses for *Digonus* are brief. Gürich (1909) listed the truncate and indented outline of the cephalic anterior margin, the angular margin of the antero-lateral corners of the cranium, the pointed pygidial tip and the weakly tapered, trapezoid glabellar outline. Reed (1918) emphasised the strong expression of the pygidial segmentation as a further diagnostic character. Sdzuy (1959) included the absence of glabellar lobation and angular pleural tips as diagnostic characters although, as he regarded *Digonus* as a subgenus of *Burmeisteria*, other characters were incorporated into the

generic concept. These included the distinct paraglabellar area, the presence of a ventral process on the rostral plate, a triangular pygidial outline, distinct pygidial trilobation, and a poorly expressed postaxial ridge. Tomczykowa (1975) omitted many of Sdzuy's characters from her revised diagnosis, closely following Reed. In emending Tomczykowa's diagnosis, Wenndorf (1990) noted the presence of weak glabellar lobation in some species, and that early representatives of the genus have less elongate pygidial outlines.

The revised diagnosis given here adds substantially to the list of diagnostic characters and qualifies other characters previously used. A substantially restricted concept of the genus is proposed by placing new emphasis on pygidial characters including the relative depth of pygidial ring and pleural furrows, the expression of the axial furrows, the expression of the postaxial ridge and the width and convexity of the pygidial axis. The revised diagnosis emphasises differences between *Digonus*, *Trimerus* and *Burmeisteria*, and results in substantially different assignments of the species listed by Tomczykowa (1975) and Wenndorf (1990).

Tomczykowa (1975) and Wenndorf (1990) considered *Digonus* to have been derived from *Trimerus*. The genera are certainly close, many of the characters listed in the diagnosis of *Digonus* occurring variously in species of *Trimerus*. Although the presence of a rostral keel or process is considered of primary importance in differentiating the genus from *Trimerus*, it is the combination of characters that defines *Digonus*. Other cephalic characters, particularly the degree of glabellar lobation, the quadrate course of the facial and rostral sutures, and the trapezoid glabellar outline, distinguish *Digonus* from most species of *Trimerus*. Pygidia of *Digonus* can generally be distinguished from those of *Trimerus* by the deeper pleural and ring furrows that are more or less equal in depth, by the shallower axial furrows, and by the less convex axis and postaxial ridge. For the morphologically convergent species, it is the continuity of the axial furrow anteriorly in *Trimerus* (and the fusion of the anteriormost axial ring and pleural rib in *Digonus*) that distinguishes the genera. Hence, *Homalonotus crassicauda* from the Emsian of Germany, known only from pygidia and previously interpreted as a temporally disjunct representative of *Trimerus* (Wenndorf, 1990, Schraut, 2000) clearly belongs in *Digonus*. The Lochkovian North American *H. major* Whitfield, 1881 is best assigned to *Trimerus* rather than to *Digonus*, because the pygidial axial furrow is deep and distinct anteriorly.

Digonus wenndorfi and *D. zeehanensis* from the lower Lochkovian of south-eastern Australia are the best known of the early representatives of *Digonus* and support the derivation of this genus from *Trimerus*. *D. wenndorfi* and the French *D. roemeri* are the earliest *Digonus*, occurring immediately above the Silurian-Devonian boundary and suggesting a latest Silurian origin for the genus. In cranial features, *wenndorfi* and *zeehanensis* show close affinities to the *D. ornatus* group from the middle Pragian-Emsian of Europe rather than to the *D. gigas* group (see Wenndorf, 1990) whose members share longer preglabellar fields. Weak glabellar lobation and short pygidia with markedly obtuse (120–130°) angular tips set *wenndorfi* and *zeehanensis* apart from later members of the

genus, with the exception of several species (*D. antarcticus* and *D. ornatus disornatus*) that retain weak lobation, and several others that have similarly short pygidia (e.g. *D. armoricanus* and *D. crassicauda*). In addition to weak glabellar lobation and short pygidial proportions, *wenndorfi* also exhibits a moderately raised pygidial postaxial ridge (Figs 12.6, 12.12–12.18). In these features *wenndorfi* can be considered a 'primitive' *Digonus*, with relict features of *Trimerus* retained. *D. zeehanensis* bears a short (sag.) but wide (tr.) median cephalic cusp (Fig. 13.1) intermediate in morphology between the large semi-circular cusps of *Trimerus* on species such as *T. (Ramiotis) otisi* and *T. (Trimerus) johannis*, and the small, acute cusps of Emsian *Digonus*. The anteriorly distinct pygidial axial furrows of *roemeri* (see Morzadec, 1986: pl. 32 figs 1, 4, 6–7) and (to a lesser extent) *wenndorfi*, can also be interpreted as a *Trimerus*-like feature, although the wide pygidial axis and equally deep pleural and ring furrows indicates their affinities with other *Digonus*.

Emphasising the significance of the transverse anterior margin of the cranidium and the depth of the pygidial pleural and ring furrows, Tomczykowa (1975) derived *Digonus* from *Trimerus*, suggesting *T. (Trimerus) johannis* as a transitional morphology between the genera. Thomas (1977) doubted this suggestion, emphasising the difference in age between *T. (T.) johannis* (late Wenlock) and the first appearance of *Digonus* (earliest Lochkovian). Wenndorf (1990) interpreted European Lochkovian species such as *Homalonotus vialai* Gosselet in Gosselet et al., 1912 and *H. roemeri* as representing early *Digonus* morphologies, noting similarities to the Polish Ludlow *T. permutus* Tomczykowa, 1978 (= *T. lobatus* Tomczykowa, 1975 non Prouty, 1923 in Swartz and Prouty). A more plausible transitional morphology is represented by the upper Ludlow *T. (Ramiotis) otisi*. The similarities of this species to contemporary *Homalonotus* have been discussed above, but its similarities to species of *Digonus* are more marked. In addition to having a tricuspid cephalic margin, *otisi* exhibits a sub-quadrate course of the facial and rostral sutures, weak glabellar lobation, straight-sided glabellar outline, deep pleural and equally deep ring furrows, and a pygidial axial furrow that is indistinct anteriorly (Fig. 20). In the latter feature, *otisi* is an exception amongst congeners. However, the flat rostral plate, the long glabellar proportions, the narrow proportions of the pygidial axis and the raised postaxial ridge demonstrate its close affinities to *Trimerus*.

Digonus wenndorfi and *D. zeehanensis* demonstrate the conservative *Digonus* cephalic morphology to have been already established in the earliest Lochkovian. European species considered by Tomczykowa (1975) as representing early *Digonus* morphologies, including *Homalonotus vialai*, *D. bostoviensis* and *D. elegans*, are variably assigned below to *Parahomalonotus* and *Wenndorfia*, and exhibit few of the diagnostic cephalic or pygidial features of *Digonus*. In particular, the anterior branches of the facial sutures of these species are broadly curved and converge at a strongly obtuse angle opposite the preglabellar field, giving the anterior margin of the cranidium a more rounded/parabolic outline. *Burmeisteria (Digonus?) delattrei* Pillet and Waterlot, 1982 from the Emsian of France exhibits few features typical of *Digonus*. It has a

raised pygidial axis, a raised postaxial ridge with a posteriorly projecting spine, anteriorly distinct axial furrows and a moderately convex (tr.), elongate glabella. The pygidial morphology, including the posteriorly projecting axis, indicates assignment to *Burmeisterella*. Wenndorf (1990) questionably assigned the Brazilian *Homalonotus oiara* Hartt and Rathbun, 1875 to *Digonus*, but their emphasis on the concavity of the sides of the glabella is not compatible with the quadrate glabellar outline considered here as diagnostic of *Digonus*. The forward eye position exhibited by the single cranidium known suggests affinities with *Burmeisteria* rather than with *Dipleura*.

Relationships between *Digonus* and *Burmeisteria* have been variously interpreted. Sdzuy (1959) considered *Digonus* to be a subgenus of *Burmeisteria*. Tomczykowa (1975) listed several differences between the taxa, emphasising the absence of spines and glabellar lobation in *Digonus* to support its independent status. Cooper (1982) argued that the range of variation in the course of the rostral suture, the degree of glabellar lobation and the glabellar outline in the highly polymorphic type species *B. herschelii* (Murchison, 1839) overlapped with morphologies typical of *Digonus*. Following the emphasis placed by Sdzuy on these characters, Cooper regarded *Digonus* as junior synonym of *Burmeisteria*. Wenndorf (1990) questioned many of the differences listed by Tomczykowa, noting a convergence in morphologies between *Burmeisteria* and *Digonus*, but nevertheless maintaining their independent status. Kennedy (1994) noted that the pygidial doublure of *Digonus*, unlike that of *Burmeisteria*, is often narrower and bears a narrow groove in the margin of the pygidial doublure. This distinction between the genera also applies to *Burmeisterella*, which Kennedy considered as a junior synonym of *Burmeisteria*. The independent status of *Burmeisterella* is supported here, with high generic significance accorded to the very short (sag.) preglabellar field and the morphology of the pygidial axis, which is raised high rather than fused with the pleural field posteriorly, and extends posteriorly over the margin as a narrow-based to spinose tip. In addition, the pygidium of *Burmeisterella* has a more convex lateral margin, and always bears a pair of prominent, large nodes or spines on the anteriormost pleural rib. The independent status of *Burmeisteria* and *Digonus* is supported in this work. The taxa can be readily distinguished morphologically, despite the extreme polymorphism exhibited by *herschelii*. In *Burmeisteria*, the pygidial axial furrow is impressed anteriorly, and the pygidial pleural and ring furrows are typically shallower than those of *Digonus* and shallow posteriorly. *Burmeisteria* is further characterised by a high number of pygidial segments (>13 axial rings). Cranidia of *Burmeisteria* and *Digonus* may exhibit morphological convergence, but a glabellar outline markedly expanded across L1-L1 (tr.) or with concave sides, and well defined lateral glabellar furrows immediately distinguish *Burmeisteria* when present.

Following Hennig (1965), Wenndorf suggested that the mutually exclusive palaeogeographic ranges of *Burmeisteria* and *Digonus* represented a significant taxonomic feature supporting their independent status. *Digonus wenndorfi*,

D. zeehanensis and *D. antarctica* extend the range of the genus into temperate palaeolatitudes of north-eastern Gondwana. However, the palaeogeographic ranges of the genera remain mutually exclusive. *B. herschelii* is restricted to lower palaeolatitudes of southern Gondwana, occurring in southern Africa, the Falkland Islands and South America. The reassignment of several South American taxa to *Burmeisteria* emphasises the provincialism of the genus (see Table 1), perhaps as early as the Late Silurian. *Homalonotus lineares* Salter, 1861, assigned below to *Burmeisteria* (see *Trimerus*) occurs in the Late Silurian of Bolivia and Uruguay.

Affinities of the Lochkovian *Homalonotus noticus* Clarke, 1913 (?= *H. caorsi* Mendez-Alzola, 1938) from South America and possibly South Africa (see Cooper, 1982) are with *Burmeisteria*. Reed (1918) initially assigned the species to *Burmeisteria* but later reassigned it to *Digonus* (Reed, 1925). Sdzuy (1957) suggested that the species represents a transitional form between *Burmeisteria* and *Digonus*. The distinct S1-S3, the narrow pygidial axis and the anteriorly continuous pygidial axial furrow are incompatible with assignment to *Digonus*. Tomczykowa (1975) and Wenndorf (1990) assigned *H. noticus* to *Trimerus*, but the presence of a rostral projection, a sinusoidal rostral suture and high pygidial segmentation (up to 13 axial rings) excludes the species from the genus as defined here.

Homalonotus clarkei from the Lower Devonian South America (?= *H. buqueti* Mendez-Alzola, 1938, ?= *H. spatulirostris* Mendez-Alzola, 1938), has been variably assigned to *Digonus* (Wolfart, 1968), to *Trimerus* (with question, Tomczykowa, 1975), to *Burmeisteria* (Cooper, 1982) and to *Dipleura* (Wenndorf, 1990). The strongly folded anterior cephalic margin excludes assignment to *Trimerus*, as this taxon is characterised in this work by having a flat rostral plate. The very shallow pygidial pleural furrows and somewhat deeper ring furrows of *clarkei* are typical of *Dipleura*, but the tricuspid anterior cephalic margin, the quadrate and medially concave anterior cranial margin, and the strong forward tapering of the glabella do not conform to this assignment. The weakly expressed pygidial segmentation excludes the species from *Digonus* as defined here. The generic affinities of the species are uncertain.

Burmeisteria (Digonus) accraensis from the Devonian of Ghana exhibits weak pygidial furrows, excluding the species from *Digonus* as defined in this work. The taxon has been variably assigned to *Trimerus* (Tomczykowa, 1975) and to *Dipleura* (with question, Wenndorf, 1990), but the presence of a rostral process (see Saul, 1967: pl. 143 fig. 6) excludes the species from these genera. The species is assigned here to *Burmeisteria*.

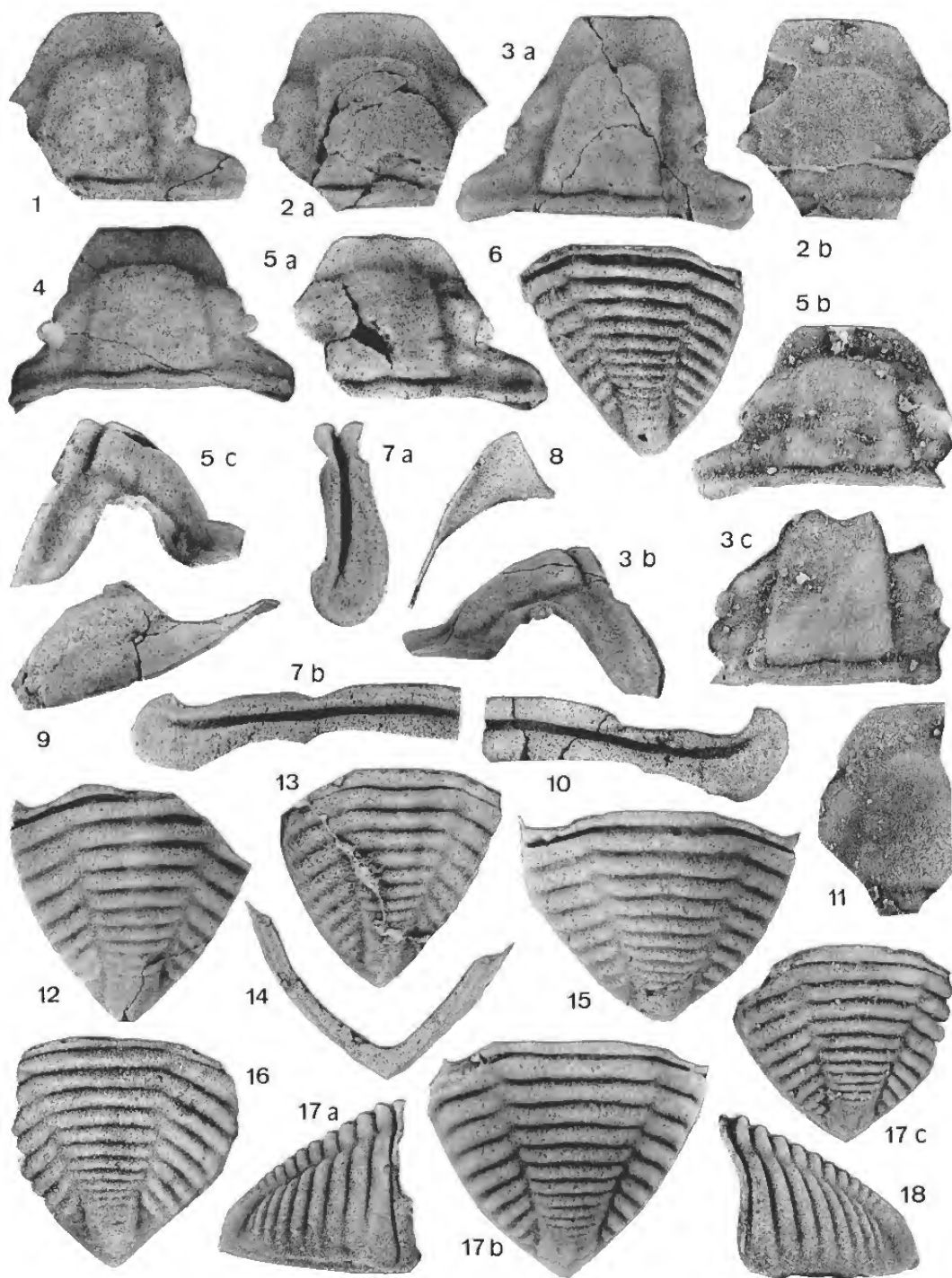
Digonus wenndorfi sp. nov.

Figs 3, 12, 22.1–22.6

Trimerus (Dipleura?) sp.—Talent, 1964: 49 (pars), pl. 26 figs 1, 2 non text-fig. 6.

Homalonotidae gen. et sp. indet. 1.—Holloway and Neil, 1982: 145, figs 4A–H.

Type material. Holotype NMV P304717 (pygidium) from PL2203, Thomas locality F3, Parish of Dargile, Heathcote, Victoria (Fig.



12.17). Paratypes NMV P304709–P304716 (cranidia), NMV P304874 (librigena), NMV P304872, P304872 (thoracic segments), NMV P304717, NMV P304860–P304866, NMV P304868 (pygidia) from PL2203. Paratype NMV P304913 (librigena) from PL2327, Heathcote. For localities see Fig. 8.

Previously figured material. NMV P78295 (ex GSV 39474, pygidium, figured Holloway and Neil, 1982: figs 4E, 4H), NMV P59656 (ex GSV 39200 pygidium, figured Talent, 1964: pl. 26 fig. 2, Holloway and Neil, 1982: figs 4F, 4G), NMV P59655 (ex GSV 39476, pygidium, figured Talent, 1964: pl. 26 fig. 1) from PL2203, NMV P78293 (thoracic segment, figured Holloway and Neil, 1982: fig. 4C), NMV P78294 (thoracic segment, figured Holloway and Neil, 1982: fig. 4D) from PL2202, Thomas locality F2, Parish of Dargile, Heathcote. NMV P78292 (cephalon, figured Holloway and Neil, 1982: figs 4A, 4B) from PL2204, Thomas locality F4, Parish of Dargile, Heathcote. For localities see Fig. 8.

Registered material. 88 specimens: 2 cephalae, 12 cranidia, 4 librigenae, 17 thoracic segments, 53 pygidia. NMV P59655, P59656, NMV P78295, NMV P82882, NMV P82886, NMV P304709–P304717, NMV P304859–P304903 from PL2203. NMV P78293, P78294, NMV P82880, NMV P82883–P82885, NMV P304904 from PL2202. NMV P82941, NMV P304905–P304914 from PL2327. NMV P78292 from PL2204.

Stratigraphic distribution. Mt Ida Formation, from about 400 m above the base of the Dealba Member up to about the 100 m above the base of the Stoddart Member, *Boucotia janae* Assemblage Zone, early Lochkovian. The first appearance of *Digonus wenndorfi* at PL2204 is close stratigraphically to the first appearance of *Boucotia* (see Garratt, 1983: fig. 7) and together support a basal Lochkovian age for these horizons.

Derivation of name. For Dr Klaus-Werner Wenndorf (Germany), for his contribution to the study of homalonotids.

Diagnosis. Glabella trapezoid, length 1.0–1.2 times width, sides straight and converging at about 20° opposite genae, anterior margin of glabella well defined with medial indentation moderately impressed to indistinct. Glabellar lobation weak to indistinct. Axial furrows moderately impressed opposite genae. Palpebral lobe short, 0.1 times cranial length, placed with midline opposite 0.5 glabellar length/0.39 cranial length. Preglabellar field long, length (sag.) 0.22 times cranial length. Rostral suture transverse. Pygidium triangular, sides moderately convex and converging posteriorly at 85–100°, tip angular. Pygidial axis with width 0.5–0.6 times pygidial width, 11–12 axial rings, ring furrows deep, continuous with raised

postaxial ridge. Axial furrows poorly defined opposite first–second axial rings, moderately impressed posteriorly, straight and tapering at 30–40°. Pleural furrows deep. 8–9 pleural ribs, rib-ring medially offset at fifth rib.

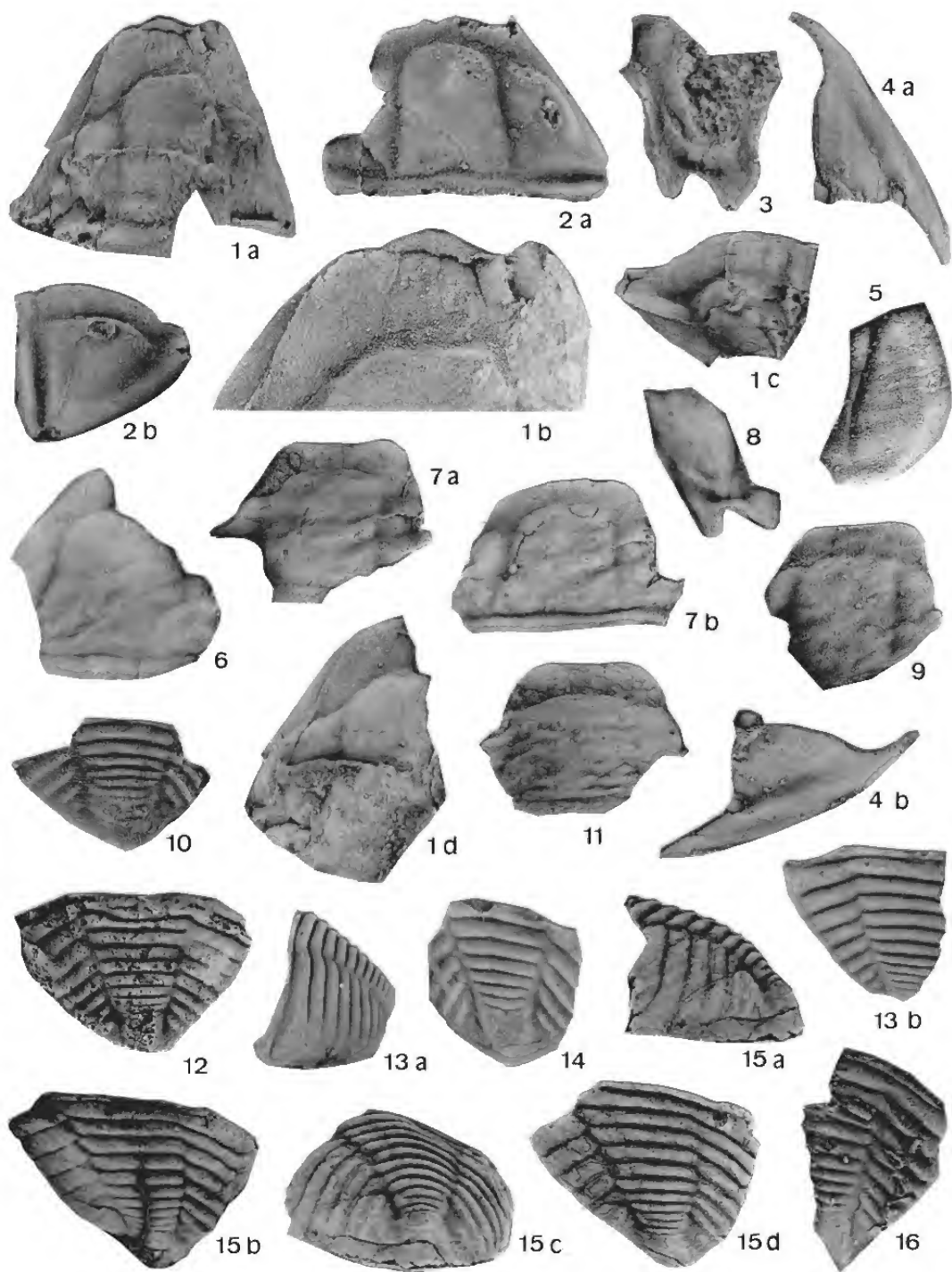
Description. Exoskeleton large (maximum length estimated 25 cm from NMV P304860), occipital convexity (tr.) moderate, pygidial convexity (tr.) strong. Dorsal exoskeleton finely granulose.

Cranidia with elongate and short forms. Elongate form with cranial width about 1.6 times length, short form with cranial width about 1.9 times length. Glabella with length 0.78 times cranial length, anterior margin very broadly rounded to transverse. Elongate form with glabellar length 1.2 times width, short form with glabellar length equal to width. Occipital ring with length 0.1 times glabellar length. Occipital furrow deeply impressed, with weak forward flexure medially. Glabellar lobation (best seen on NMV P304715 and NMV P304710) with L1 0.28 and L2 0.15 times glabellar length respectively. S1 straight and directed posteromedially at about 17° from the transverse, S2 weakly convex forwards and transverse, S3 indistinct. In some specimens (e.g. NMV P304710, P304711) S1 moderately impressed for short distance adjacent to axial furrow. Axial furrows very shallow and directed diagonally opposite occipital ring. Paraglabellar area weakly defined (best seen on NMV P304711). Length (exsag.) of posterior border equal to occipital length adaxially, lengthening slightly abaxially. Posterior border furrow transverse, very wide, moderately impressed, terminating distally. Postocular fixigenal area very short, length (exsag.) 0.16 times cranial length. Palpebral lobes placed remotely (δ - δ 1.67 times preoccipital glabellar width/0.7 times cranial width). Palpebral furrow weak to moderately impressed. Preocular fixigenal area of moderate width, 0.17 times δ - δ narrowing slightly anteriorly. Preglabellar field weakly concave (tr. sect.). Anterior branches of facial suture angular, directed exsagittally for a short distance adjacent to the eye (to a point opposite 0.7 glabellar length), anteriorly converging at about 40° in elongate forms and 60° in short forms. Librigena without distinct border furrow or lateral border. In anterior view anterior margin of librigenae moderately convex.

Thorax with axial furrows indistinct. Pleural furrows wide and deep.

Pygidia with long form and narrow form, sides converging posteriorly at about 85° in narrow form and 100° in wide form. Pygidial axis with width about 0.5 times pygidial width in wide form, 0.6 in narrow form. Pygidial axis reaching to about 0.85 times pygidial length, raised, continuous posteriorly with postaxial ridge. Postaxial ridge wide, width 0.3 times axial width. Axial furrows straight and tapering at about 33° in narrow form, 38° in wide form, curving to the exsagittal posteriorly. Pleural furrows not reaching margin. Border furrow and border not defined. In posterior view posterior margin of pygidium

Figure 12. *Digonus wenndorfi* sp. nov. 1, paratype NMV P304715, cranidium, dorsal view $\times 1.25$ (internal mould) from PL2203. 2a, paratype NMV P304714, cranidium, dorsal view $\times 1.6$ (internal mould) from PL2203. 2b, same (latex cast). 3a, paratype NMV P304709, cranidium, dorsal view $\times 0.75$ (internal mould) from PL2203. 3b, same, lateral view (latex cast). 4, paratype NMV P304716, cranidium, dorsal view $\times 1.2$ (internal mould) from PL2203. 5a, paratype NMV P304711, cranidium, dorsal view $\times 1.75$ (internal mould) from PL2203. 5b, same (latex cast). 5c, same, oblique view (internal mould). 6, paratype NMV P304868, pygidium, dorsal view $\times 1.0$ (internal mould) from PL2203. 7a, paratype NMV P304872, thoracic segment, lateral view $\times 2.3$ (internal mould) from PL2203. 7b, same, dorsal view. 8, paratype NMV P304874, librigena, ventral view (double) $\times 1.75$ (latex cast) from PL2203. 9, paratype NMV P304913, librigena, lateral view $\times 1.7$ (internal mould) from PL2327. 10, paratype NMV P304873, thoracic segment, dorsal view $\times 2.0$ (internal mould) from PL2203. 11, paratype NMV P304712, cranidium, dorsal view $\times 1.25$ (latex cast) from PL2203. 12, paratype NMV P304864, pygidium, dorsal view $\times 1.4$ (internal mould) from PL2203. 13, paratype NMV P304861, pygidium, dorsal view $\times 1.8$ (latex cast) from PL2203. 14, paratype NMV P304860, pygidium, ventral view (double) $\times 1.25$ (internal mould) from PL2203. 15, paratype NMV P304863, pygidium, dorsal view $\times 1.5$ (internal mould) from PL2203. 16, paratype NMV P304865, pygidium, dorsal view $\times 1.7$ (latex cast) from PL2203. 17a, holotype NMV P304717, pygidium, lateral view $\times 1.1$ (internal mould) from PL2203. 17b, same, dorsal view $\times 1.3$. 17c, same, $\times 1.1$ (latex cast). 18, paratype NMV P304862, pygidium, lateral view $\times 1.5$ (internal mould) from PL2203.



horizontal. In lateral view dorsal profile of axis inclined at about 30° to the horizontal, postaxial ridge very steeply inclined.

Discussion. *Digonus wenndorfi* is abundant and dominates the trilobite fauna at several localities. Except for a cephalon (Holloway and Neil, 1982: figs 4A, 4B) the species is known only from isolated tergites. Relative proportions of many features (eg. glabellar and pygidial length/width ratios) are difficult to ascertain due to deformation. Nevertheless, two distinct forms of *wenndorfi* can be recognised, elongate and short morphs differing in the relative proportions of the cephalon, glabella and pygidium. These morphs are not related to size, nor are they products of deformation as their ranges in size overlap, and they occur together on the same bedding plane (Fig. 3). The differing morphological proportions within the population are strongly bimodal rather than continuous. Pygidial length-width ratios range between 0.76–0.93 (average 0.86) in the short morphs, in the long morphs between 1.11–1.12. Similarly, glabellar length-width ratios range between 0.96–1.00 (average 0.99) in the short morphs, in the long morphs between 1.15–1.23 (average 1.19). Similar observations have been made for populations of *D. gigas* and attributed to sexual dimorphism (Dahmer, 1914), although Wenndorf (1990: table 31) demonstrated, with a much larger sample size of 67 pygidia, that the variation in *gigas* is continuous rather than bimodal, with intermediate forms being the most numerous, and so not reflecting sexual dimorphism. Although the sample size for *wenndorfi* is much smaller (11 measurable specimens) the complete absence of intermediate forms (e.g. pygidia with length-width ratios range between 0.93–1.1) is statistically significant. Whether the bimodality reflects sexual dimorphism is uncertain, although the narrower morphs strongly outnumber the wider morphs and so suggest that it does not.

The subquadrate outline of the anterior part of the cranium, the weakly tapered trapezoid glabellar outline, the wide pygidial axis, and the depth of the pygidial ring and pleural furrows clearly indicate assignment to *Digonus*. *D. wenndorfi* differs markedly from the *D. gigas* group and more closely resembles the *D. ornatus* group in having a relatively longer preglabellar field, wide fixigenae anteriorly, and a transverse rather than weakly concave anterior cranial margin.

Digonus wenndorfi differs from most Pragian-Emsian species of *Digonus* in lacking the elongate, straight-sided tri-

angular outline and a long produced tip characteristic of the type and other taxa such as *D. ornatus* and *D. intermedius*. In having shorter pygidial proportions, *wenndorfi* more closely resembles other Lochkovian species, including *D. laticaudatus* from North America, *D. armoricanus* from France, and *D. roemeri* from Europe. Compared to Pragian-Emsian species, Lochkovian species of *Digonus* lack some of the features characterising *Digonus*. These species can be interpreted as reflecting ancestral morphologies, as might be expected in the earliest representatives of a genus. 'Trimerus-like' features including the raised postaxial ridge and weak glabellar lobation of *wenndorfi* can be interpreted in this context.

Of Lochkovian species of *Digonus*, only *D. zeehanensis* from Tasmania (redescribed below) is known sufficiently for detailed comparison with *D. wenndorfi*. These taxa are very close, but the latter differs in having slightly concave glabellar sides, a longer glabella, more distinctly expressed glabellar lobation, a shorter preglabellar field, a much shorter pygidium with a relatively narrower pygidial axis, a more obtusely-angled pygidial tip, and a lower postaxial ridge (Fig. 13). With the exception of the latter, these features suggest that *zeehanensis* represents a less derived morphology.

Digonus roemeri is a near-contemporary of *D. wenndorfi*, recorded from the base of the Lochkovian (*hesperius* zone) in Europe (Chlupáč et al., 2000). The species is poorly documented and, as noted by Tomczykowa (1975), a number of taxa have been assigned to it. Topotypes of *D. roemeri* (Morzadec, 1986: pl. 32 figs 1, 4, 6–10) share with *wenndorfi* short pygidial proportions and the equally deep pygidial pleural and ring furrows typical of *Digonus*. *D. roemeri* differs from *wenndorfi* in that the pygidial axis is wider and the postaxial ridge is not raised. In contrast to other species assigned to the genus, pygidia of *roemeri* and the comparable *D. laticaudatus* exhibit anteriorly continuous pygidial axial furrows, interpreted here to reflect the ancestral morphology.

Many species assigned to *Digonus* are poorly documented and comparison with *D. wenndorfi* is difficult. From Europe, *D. harpyius* is known only from a rostral plate. The Emsian *D. goniopygaeus* from England and *D. crassicauda* from Germany are known only from pygidia. Despite the comparable short proportions, the pygidium of *crassicauda* differs from that of *wenndorfi* in having a weakly defined postaxial ridge and a narrow, recurved flange defining the pygidial tip (Wenndorf, 1990: pl. 9 figs 1–3), as in other Emsian *Digonus*. The Antarctic *D. antarcticus* differs markedly from *wenndorfi*

Figure 13. *Digonus zeehanensis* (Gill, 1949). 1a, NMV P304656, cephalon, dorsal view $\times 1.2$ (internal mould) from PL1726. 1b, same, enlargement of anterior margin $\times 2.5$. 1c, same, lateral view of cephalon $\times 1.0$. 1d, same, dorsal view $\times 1.25$ (latex cast). 2a, NMV P304657, cephalon, dorsal view $\times 2.6$ (internal mould) from "Little Henty River". 2b, same, lateral view $\times 2.25$. 3, NMV P304650, hypostome, ventral view $\times 2.2$ (internal mould) from PL1726. 4a, NMV P304653, librigena, dorsolateral view $\times 1.3$ (latex cast) from PL1726. 4b, same, lateral view. 5, NMV P304652, thoracic segment, lateral view $\times 3.0$ (latex cast) from PL1726. 6, NMV P14789, cranium, dorsal view $\times 0.9$ (latex cast) from PL1726. 7a, holotype NMV P14590, cranium, dorsal view $\times 1.3$ (latex cast) from PL1726. 7b, same, internal mould $\times 1.1$. 8, NMV P304683, hypostome, ventral view $\times 2.1$ (latex cast) from PL1726. 9, NMV P304658, cranium, dorsal view $\times 1.6$ (latex cast) from PL6653. 10, NMV P304649, pygidium, dorsal view $\times 1.1$ (internal mould) from PL1726. 11, NMV P304655, cranium, dorsal view $\times 1.0$ (latex cast) from PL1726. 12, NMV P7651, pygidium, dorsal view $\times 1.65$ (internal mould) from "Mt Zeehan". 13a, NMV P304648, pygidium, lateral view $\times 1.1$ (internal mould) from PL1726. 13b, same, dorsal view. 14, NMV P14787, pygidium, dorsal view $\times 0.75$ (latex cast) from PL1726. 15a, paratype NMV P14592, pygidium, lateral view $\times 1.0$ (internal mould) from PL1726. 15b, same, dorsal view (latex cast). 15c, same, dorsoposterior view (internal mould). 15d, same, dorsal view. 16, NMV P304659, pygidium, dorsal view $\times 1.0$ (latex cast) from "Mt Zeehan".

in having weakly expressed pygidial axial furrows, exceptionally deep pleural furrows and a poorly expressed postaxial ridge (Saul, 1965: pl. 17 figs 1–11).

Holloway and Neil (1982) considered specimens of *Digonus wenndorfi* to be close to *Trimerus lilydalensis* Gill, 1949, also from the Lochkovian of central Victoria. The availability of many new specimens of *wenndorfi* and a revision of Gill's species does not support this comparison, with the latter assigned to the new genus *Wenndorfia*.

Digonus zeehanensis (Gill, 1949)

Figure 13

Trimerus zeehanensis Gill, 1949: 70, pl. 9 figs 1, 2, 4, text-fig. 1D.—Tomczykowa, 1975: 11.—Wenndorf, 1990: 16.—Holloway and Sandford, 1993: 93.—Schraut, 2000: 382.

Type material. Holotype NMV P14590 (cranium, counterpart previously registered NMV P14591, Fig. 13.7) and paratype NMV P14592 (pygidium, counterpart previously registered NMV P145913) from PL1726, Gill and Banks locality 16, Zeehan, Tasmania.

Registered material. 67 specimens: 2 cephalae, 13 cranidia, 12 librigenae, 2 hypostomes, 11 thoracic segments, 27 pygidia. NMV P14787, P14788 (counterparts), NMV P14789, NMV P14791, NMV P304648–P304656, NMV P304662, NMV P304664–P304708 from PL1726. NMV P304657 from "Little Henty River", Zeehan. NMV P304661 from "near Little Henty River", Zeehan. NMV P304663 from PL1725, Gill and Banks' locality 15, Zeehan. NMV P304660, NMV P304658 from PL6653, Zeehan. NMV P7561, NMV P304659 from "Mt Zeehan", Zeehan.

Stratigraphic distribution. Bell Shale, *Boucotia australis* Assemblage Zone, mid-late Lochkovian.

Diagnosis. Cephalon trapezoid, sides straight, anterior margin tricusate, with short (0.05 times cephalic length) but wide (length 0.25 times width) median cusp, lateral cusps about half the length of the median cusp. Glabella trapezoid, sides weakly concave and converging at about 20°, length about 1.2 times width, anterior margin well defined, lobation weakly defined. Axial furrows moderately impressed. Palpebral lobe placed with midline opposite 0.52 glabella length/0.42 cranidia length. Preglabellar field with length (sag.) 0.17 times cranidia length. Anterior branches of facial suture straight and converging at about 50°, curving abruptly to the exsagittal anteriorly. Rostral suture transverse. Dorsal surface of rostral plate triangular, short, length 0.15 times width. Hypostome with middle furrow deep adaxially, shallow abaxially. Posterior border of hypostome with long lateral lobes of length 0.17 times hypostomal length. Pygidium short, length 0.68 times width, sides moderately convex and converging posteriorly at about 110°. Pygidial axis 0.45 times pygidial width, 12 axial rings, continuous with low postaxial ridge. Axial furrows tapering at about 30°, moderately impressed posteriorly, not continuous anteriorly opposite first ring. Pleural and ring furrows deep. 8 ribs, rib-ring medially offset at fifth rib. Dorsal exoskeleton with coarse pitting.

Discussion. The Bell Shale is strongly sheared, resulting in wide variations in shapes and proportions of specimens. Because Gill (1949) described the species from a limited

number of specimens, examination of a larger population reveals a number of inaccuracies in his description. The concavity of the preglabellar field and the upturning of the anterior cranial margin on the holotype (Fig. 13.7), considered diagnostic of the species by Gill, are features attributable to tectonic distortion and are absent from other topotype cranidia. Gill recorded lateral glabellar furrows as absent, but they are weakly defined on most specimens. The pygidial axial furrows are moderately impressed rather than poorly defined. Despite the abundance of cephalic and pygidial tergites, thoracic pleurae are unusually rare in the Bell Shale. From the fragments available, there is no indication of spines on the thorax as suggested by Gill.

Tomczykowa (1975) and Wenndorf (1990) assigned Gill's species to *Trimerus*, but the quadrate course of the anterior branches of the facial and rostral sutures, the equally deep pygidial ring and pleural furrows and the effacement of the axial furrow anteriorly are more consistent with an assignment to *Digonus*. Pygidia have a much wider axis (average width 0.46 pygidial width) than recorded by Gill, who cited the axial width to be one third the pygidial width. However, as noted above, the longer glabellar proportions, more distinctly expressed glabellar lobation, shorter pygidial proportions with a relatively narrower axis and a more obtusely-angled pygidial tip suggest that *D. zeehanensis* represents a less derived morphology compared to other *Digonus*. In these features, *zeehanensis* is most closely comparable to *D. roemeri* from the basal Lochkovian of France.

Environmental notes. *Digonus zeehanensis* dominates the trilobite fauna of the Bell Shale. At the best-sampled locality (PL1726), the relative abundance of *D. zeehanensis* is >90%. The fauna is typical of homalonotid-dominated assemblages, being low diversity and otherwise comprising a proetid, a cheirurid and a dalmanitid (Gill, 1950). The latter suggests alignment with the deeper water *Trimerus delphinocephalus-Dalmanites limulurus* Community of Mikulic, 1999. The proportion of articulated specimens in populations of *zeehanensis* is low. Of the 67 specimens, all are isolated tergites with the exception of three cephalae. Breakage is high in the sampled populations (Br=27%). Specimens occur on bedding planes in association with other fossil concentrations or in more sparsely fossiliferous layers between the lag bands. The taphonomy is indicative of taphofacies TIII and together with the lithofacies and biofacies suggests a setting around maximum storm wave base.

Dipleura Green, 1832

Type species: *Dipleura dekayi* Green, 1832. From the Middle Devonian Hamilton Group, New York State, USA, by monotypy.

Other species included. *Dipleura boliviensis* Wolfart, 1968, *D. garatti* sp. nov., *D. iberica* Wenndorf, 1990, *Homalonotus kayseri* Thomas, 1905, *H. laevicauda* Quenstedt, 1852, = *H. simplex* Richter and Richter, 1926, *D. lanvoienensis* Morzadec, 1969, *D. praecox* Tomczykowa, 1975, *D. sp.* (in Richter and Richter, 1943), *D. sp.* (in Morzadec, 1981), *D. sp. nov.* (in Wenndorf, 1990).

Range. Upper Silurian (mid Ludlow)-Middle Devonian (Givetian).

Revised diagnosis. Cephalon short, length 0.5 to 0.6 times cephalic width, rounded triangular to semicircular in outline. Glabella with sides straight or weakly concave, subparallel to moderately convergent (20°), length 1.1 to 1.25 times width, without lobation in maturity. Preglabellar field of moderate length, 0.15–0.18 times cranial length. Paraglabellar areas indistinct. Palpebral lobes posteriorly placed, opposite 0.3 to 0.45 cranial length. Eyes remote, δ - δ generally 1.7–1.9 times preoccipital glabellar width. Anterior branches of facial sutures describing a broad curve and strongly convergent anteriorly, between 80 – 100° opposite midlength of preglabellar field. Rostral suture transverse to moderately convex forwards. Ventral surface of rostral plate flat, without projection. Pygidium with weakly defined trilobation, axial furrows very shallow to effaced. Axis with ring furrows moderately impressed to effaced, with weak to distinct posterior swelling, without well defined postaxial ridge. Pleural furrows shallow to effaced, invariably as shallow or shallower than ring furrows. Finely papillate ornament.

Discussion. As with *Digonus*, *Parahomalonotus* and *Burmeisteria*, the type species of *Dipleura* is one of the youngest members of the genus and differs significantly from older forms. General morphological changes in the genus over time include a trend toward a less tapered glabellar shape with increasingly concave sides, and a decrease in the definition of pygidial segmentation and trilobation. In Middle Devonian species a stronger cephalic convexity is developed, and the contrast in depth between ring furrows and pleural furrows is not as marked. The revised diagnosis differs from previous ones in recognising the limited significance that pygidial outline holds as a generic character. In the case of *Dipleura*, the oldest (early Ludlow) species, *Dipleura garratti* from Victoria, has a long, acuminate triangular-shaped pygidium with an acutely pointed tip, in contrast to the short parabolic outline and rounded pygidial tip exhibited by Devonian taxa and considered characteristic of the genus. The upper Ludlow *D. praecox* from Poland has an intermediate morphology, having a short triangular outline with an angular tip.

Emphasis is placed on several characters listed by Salter (1865), Reed (1918) and Sdzuy (1959) but omitted by Tomcykova (1975) and Wenndorf (1990). These include the course of the facial and rostral sutures, eye position and weak expression of paraglabellar areas. Several new diagnostic characters are added, including the absence of a projection or keel on the ventral surface of the rostral plate, the presence of a weak to distinct posterior swelling of the pygidial axis and the absence of a well defined postaxial ridge.

The revised concept of the genus excludes a number of species that have been previously assigned to *Dipleura* (see Wenndorf, 1990: table 1, Tomcykova, 1975: table 3). These include *Burmeisteria* (*Digonus*) *accraensis* from West Africa, *Homalonotus clarkei* from Bolivia, *Dipleura salteri* Morris, 1988 from England and *Trimerus* (*Dipleura*) *fornix* Haas, 1968 from Turkey. Generic assignment of the two former species is discussed under *Digonus*. *D. salteri* is tentatively assigned to *Trimerus* (*Ramiotis*), discussed below. *T. (D.) fornix* is assigned

below to *Wenndorfia*, erected for many of the species previously assigned to *Parahomalonotus*. Cephalic outline, the stronger segmentation of the pygidial axis compared to the pleural field, and the definition of the pygidial axial furrow posteriorly were considered by Wenndorf (1990) to be important generic characters in distinguishing *Dipleura* from morphologically convergent species of *Parahomalonotus*. In restricting *Parahomalonotus* to a group close to the type species, the distinction between the two genera is marked. In particular, the strong glabellar and pygidial axial convexity, strong glabellar lobation and strong pygidial segmentation easily separate members of *Parahomalonotus* s.s. from those of *Dipleura*. The problem of convergence addressed by Wenndorf re-emerges however, between *Dipleura* and species assigned below to *Wenndorfia*. *Dipleura* and *Wenndorfia* share many characters including a weakly tapering glabellar outline, effaced glabellar lobation, a posterior eye position, a preglabellar field of moderate length, an effaced pygidial postaxial ridge and pygidial outlines that are for the most part rounded parabolic. For the latter character triangular outlines are exceptional, expressed in early representatives of each genus such as *D. garratti* and *W. lilydalensis* (Gill, 1949). Many species assigned to *Wenndorfia* can be immediately distinguished from *Dipleura* in having distinct pygidial segmentation, with pleural furrows being moderately to deeply impressed. Such species include *W. multicastratus* (Koch, 1883a), *W. miloni* (Renaud, 1942), *W. elegans* (Tomcykova, 1975), *W. bostoviensis* (Tomcykova, 1975), *W. plana junior* (Wenndorf, 1990) and *W. sp.* (= *Digonus vialai* in Tomcykova, 1975). However, in a number of taxa the pygidial axial and pleural furrows are weakly impressed to indistinct, including *W. plana plana* (Koch, 1883a), *W. forbesi* (Rouault, 1855) and *W. fornix*. Assignment of these convergent species to *Wenndorfia* is indicated by consistent differences in the course of the facial sutures between *Dipleura* and *Wenndorfia*. In *Dipleura*, the facial sutures tend to be more strongly convergent and the rostral suture more forwardly convex, giving a more parabolic or V-shaped outline to the anterior margin of the cranidium. By contrast, the rostral suture of *Wenndorfia* is transverse or weakly convex forwards. The anterior branches of the facial sutures tend to be less strongly convergent posteriorly, abruptly curved medially and more strongly convergent anteriorly, giving the anterior margin of the cranidium a more rounded, U-shaped outline.

Reed (1918) suggested that *Dipleura* was derived from *Digonus*. More recent phylogenies are in accord in deriving *Dipleura* directly from *Trimerus*, although there is disagreement in the chronology of this transition. Sdzuy (1957: fig. 3) considered *Dipleura* to have originated from *Trimerus* at the Siluro-Devonian boundary. Tomcykova (1975) established an earlier origin for *Dipleura*, and suggested two species from the upper Ludlow of Poland, *Dipleura praecox* Tomcykova, 1975 and *Trimerus permutus* Tomcykova, 1978 from the immediately underlying beds, to be closely related and to represent a transitional link between the genera. An earlier origin for *Dipleura* is indicated by its occurrence in lower Ludlow strata of Victoria, supporting Wenndorf's (1990: fig. 6) suggestion of a Wenlock origin for the genus.

Dipleura is presumably derived from Lower Silurian

Trimerus. Lower Silurian *Trimerus* are variably assigned in this work to *T. (Trimerus)* or to *T. (Ramiotis)*. *T. (Trimerus)* is characterised by a suite of distinctive cephalic and pygidial features, notably a glabellar outline markedly expanded across L1-L1 (tr.), raised glabellar profile, the strongly-defined glabellar lobation, L1-L2 muscle scars, sagittal ridge, exsagittal furrows and paraglabellar areas, the long and weakly concave (tr.) preglabellar field, and the produced pygidial tip. In the absence of most of these features species assigned to *T. (Ramiotis)* more closely resemble *Dipleura*. Llandovery species of *T. (Ramiotis)* exhibit features that show a strong resemblance to those typical of *Dipleura*, sharing trapezoid glabellar outlines, shorter preglabellar fields and marked contrast between the depth of the ring furrows and pleural furrows, with the latter very shallow to almost effaced.

Sdzuy (1957) interpreted *Homalonotus (Trimerus) mongolicus* Tchernycheva, 1937 from the Upper Silurian of Mongolia as an intermediate form between *Dipleura* and *Trimerus*. Sdzuy emphasised the posterior eye position, the rounded pygidial outline and the marked contrast between the depth of the ring furrows and almost effaced pleural furrows to support his interpretation. The significance of these characters is overstated by Sdzuy. The markedly weak pleural furrows and rounded pygidial outline of *mongolicus* emphasised by Sdzuy are not features unique to *Dipleura* and occur amongst species of *T. (Ramiotis)* and *T. (Edgillia)*. The eyes of *mongolicus* are clearly placed directly opposite the glabellar midlength (Tchernycheva, 1937: pl. 1 fig. 8). The rounded pygidial outline emphasised by Sdzuy is contradicted by Tchernycheva's description of the pygidium as "*triangular, usually elongated, terminates in a thick spine*" (Tchernycheva, 1937: 25). In strong contrast to *Dipleura*, the species exhibits a very long preglabellar field (0.3 cranial length) and the anterior branches of the facial sutures are relatively weakly convergent (60°). Tchernycheva's description of other features including a subquadrate, weakly tapering glabellar outline, an evenly vaulted glabellar profile, weak S1 and indistinct S2 and S3, 13 pygidial axial rings, shallow pygidial pleural furrows, the absence of a postaxial ridge ("*rhachis falling short of posterior margin*") and the pygidial proportions (length 0.92 width) indicate assignment to *T. (Edgillia)*.

Dipleura garratti sp. nov.

Figure 14

Homalonotus sp.—Chapman, 1908: 220.

Figure 14. *Dipleura garratti* sp. nov. 1, paratype NMV P308638, cranidium, dorsal view $\times 3.0$ (internal mould) from PL6615. 2, paratype NMV P308645, cephalon, dorsal view $\times 3.0$ (latex cast) from PL6615. 3, paratype NMV P308646, pygidium, dorsal view $\times 3.8$ (internal mould) from PL6615. 4a, paratype NMV P308663, cephalon, ventral view (doublure) $\times 4.1$ (latex cast) from PL6614. 4b, same, enlargement of rostral plate $\times 15$. 5, paratype NMV P308641, cranidium, dorsal view $\times 3.0$ (internal mould) from PL6615. 6, paratype NMV P308642, cephalon, dorsal view $\times 2.2$ (internal mould) from PL6615. 7, paratype NMV P308643, librigena, ventral view (doublure) $\times 2.6$ (latex mould) from PL6615. 8, paratype NMV P308657, cranidium, dorsal view $\times 1.9$ (internal mould) from PL6614. 9, paratype NMV P308649, cephalon, dorsal view $\times 2.0$ (internal mould) from PL6614. 10a, paratype NMV P308635, cephalothorax, dorsal view of cephalon $\times 2.2$ (internal mould) from PL6614. 10b, same, dorsal view of thorax $\times 2.0$. 11, paratype NMV P308639, cephalon, dorsal view $\times 1.8$ (internal mould) from PL6615. 12, paratype NMV P308640, pygidium, dorsal view $\times 3.5$ (internal mould) from PL6615. 13a, holotype NMV P308644, pygidium, dorsal view $\times 2.1$ (internal mould) from PL6615. 13b, same, posterior view. 13c, same, lateral view $\times 2.8$. 14, paratype NMV P308648, cephalon, oblique view $\times 3.0$ (latex cast) from PL6614. 15, paratype NMV P308637, pygidium, dorsal view $\times 3.5$ (internal mould) from PL6615. 16, paratype NMV P308636, cephalothorax, lateral view $\times 3.0$ (internal mould) from PL6614. 17, paratype NMV P308651, cephalon, dorsal view $\times 3.3$ (internal mould) from PL6614.

Type material. Holotype NMV P308644 (pygidium) from PL6615, Eden Park, Victoria (Fig. 14.13). Paratypes NMV P308638, NMV P308641 (cranidia), NMV P308639, NMV P308642, NMV P308645 (cephala), NMV P308643 (librigena), NMV P308637, NMV P308640, NMV P308646 (pygidia) from PL6615. Paratypes NMV P308635-6 (cephalothoraxes), NMV P308649, NMV P308651, NMV P308663, (cephala), NMV P308657 (cranidium) from PL6614, Eden Park. NMV P308648 from "Whittlesea", Victoria. For localities see Fig. 11.

Registered material. 47 specimens: 4 cephalothoraxes, 8 cephal, 17 cranidia, 2 librigenae, 2 thoracic segments, 14 pygidia. NMV P304513–P304515, NMV P304572, P304573, NMV P308633–P308636, NMV P308649–P308657, NMV P308673 from PL6614. NMV P308637–P308647, NMV P308659–P308672 from PL6615. NMV P308658 from PL6625, Wandong, Victoria. NMV P308648 from "Whittlesea". Unregistered specimens from PL1793, Clonbinane and Kenley locality 14c, Upper Plenty. For localities see Fig. 11.

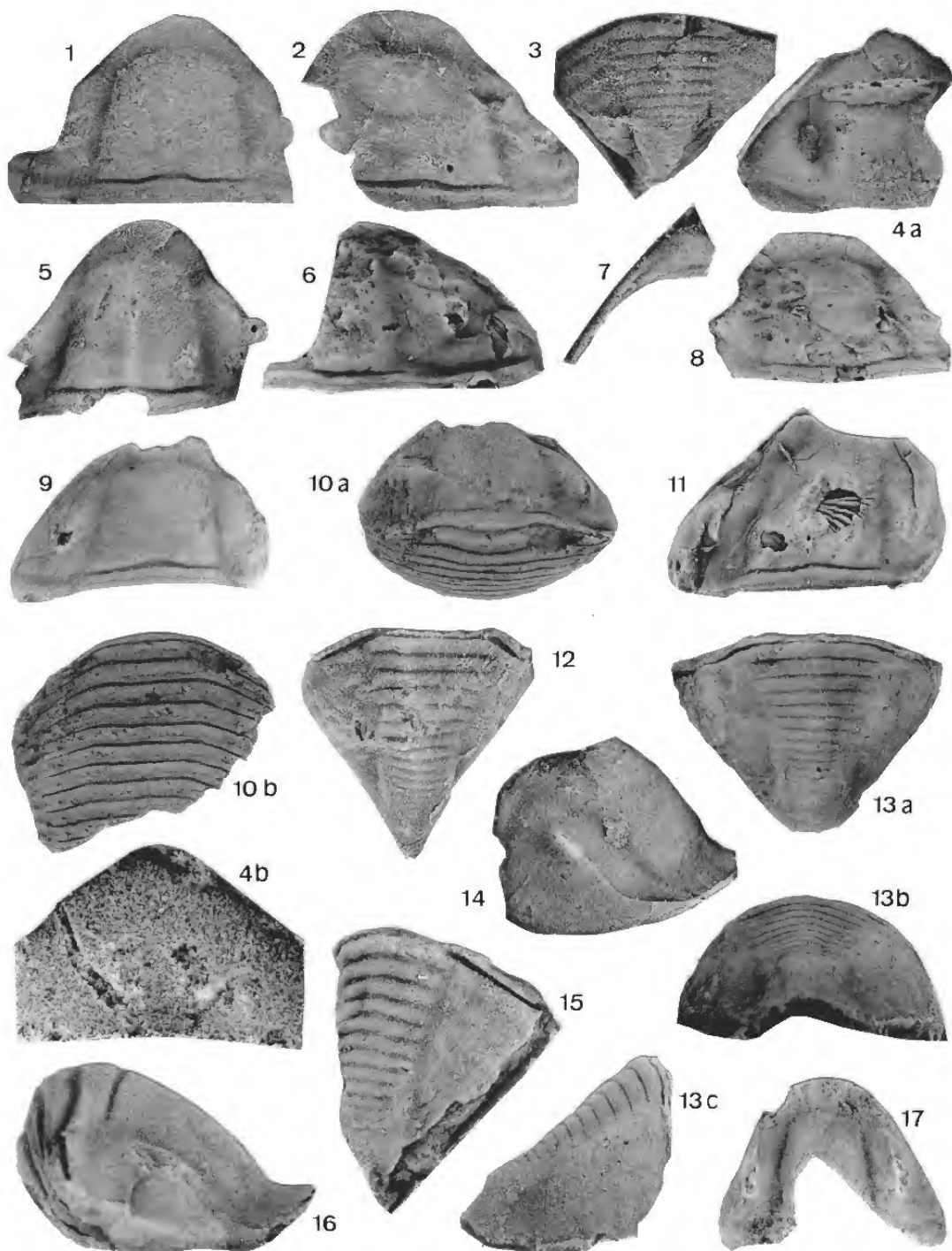
Stratigraphic distribution. As for *Homalonotus williamsi*.

Derivation of name. For Michael J. Garratt, for his contribution to Victorian palaeontology and stratigraphy.

Diagnosis. Glabella trapezoid, length 1.05 times preoccipital glabellar width, sides straight and converging at about 25°, anterior margin well defined, very broadly rounded to transverse. Length (sag.) of preglabellar field 0.15–0.18 times cranial length. Palpebral lobe placed with midline opposite 0.47 times glabellar length/0.38 times cranial length. Anterior branches of facial suture angular, subparallel to axial furrows to a point opposite 0.75 glabellar length, anteriorly converging at about 80°. Rostral suture broadly curved. Ventral surface of rostral plate with length about equal to width, flat, connective sutures angular, anterior section converging at 40 degrees, posterior section at 80°. Pygidium triangular, length equal to width, sides straight and converging at 65°, tip acutely angular. Pygidial axis with width 0.5 times pygidial width, 12 axial rings, ring furrows moderately impressed, axis moderately swollen posteriorly, continuous with wide but poorly defined postaxial ridge. Axial furrows straight and tapering at about 33°, weakly impressed to indistinct. Pleural furrows weakly impressed to indistinct. 6 pleural ribs, rib-ring medially offset at second rib.

Description. Exoskeleton small (maximum length estimated 8 cm from NMV P308644), occipital and pygidial convexity (tr.) moderate. Dorsal exoskeleton finely granulose.

Cephalon with width about 1.6 times length, with semielliptic outline, sides moderately convex. Cranial width about 1.64 times length.



Glabella length about 0.8 times cranial length. Occipital ring 0.12 times glabella length, slightly wider medially. Occipital furrow deeply impressed, with weak forward flexure medially. Glabella lobation extremely weak to indistinct, best seen on NMV P308638 as very shallow depression at adaxial end of S1 placed opposite 0.3 times glabella length. Paraglabellar area very weakly defined. Length (exsag.) of posterior border equal to occipital length adaxially, lengthening slightly abaxially. Posterior border furrow transverse adaxially, curving gently forwards abaxially, very wide, moderately impressed, terminating distally. Postocular fixigenal area very short, length (exsag.) 0.15 times cranial length. Palpebral lobes placed remotely (δ - δ 1.65 times preoccipital glabella width). Palpebral lobe length (exsag.) 0.15 times cranial length, palpebral furrow indistinct. Preocular fixigenal area of moderate width, 0.18 δ - δ , narrowing slightly anteriorly, eye ridges very weakly defined. Librigena without distinct border furrow or lateral border. Dorsal surface of rostral plate very short (sag.), crescentic in outline. Ventral surface of rostral plate kite-shaped, posterior width 0.2 times maximum width. Hypostomal suture extremely weakly curved.

Thorax with thirteen segments. Axial furrows extremely shallow, expressed as diagonally directed furrows on each segment, each meeting posterior margin at axial articulating process on internal mould. Pleural furrows wide and deep across axis, narrower (exsag.) and deeper across pleural field.

Pygidial border furrow and border poorly defined. In posterior view posterior margin of pygidium horizontal. In lateral view dorsal profile evenly inclined, interrupted by swelling of terminal piece.

Discussion. The assignment of this species to *Dipleura* is indicated by the course of the facial sutures (anterior branches converging at 90°), the posterior position of the eye and the almost effaced pygidial axial furrows and pleural furrows. The short preglabellar field and indistinct glabella lobation are in accord with this assignment. *D. garratti* is the earliest representative of the genus. A number of differences with later *Dipleura* can be interpreted as reflecting the closer affinities of *garratti* with *Trimerus*, particularly its triangular pygidial outline and its posteriorly raised axis that is continuous with a wide postaxial ridge (Fig. 14.12).

In many features *Dipleura garratti* is most closely comparable to the German upper Pragian-lower Emsian *D. laevicauda*, sharing a moderately tapered glabella outline, more elongate pygidial proportions and a relatively wide pygidial axis. The course of the cephalic sutures is most like that of the Bolivian Givetian *D. boliviensis*. Originally described as a subspecies of *D. dekayi*, the relatively longer cephalic proportions, more tapering glabella, more anteriorly and less remotely placed eyes are significant in regarding *boliviensis* as an independent species.

Environmental notes. *Dipleura garratti* occurs in a trilobite fauna dominated by proetids and dalmanitids, with *Homalonotus williamsi*, aulacopleurids, odontopleurids and phacopids in very low abundance. Although known from various localities between Clonbinane and Eden Park, the fauna is well represented at two richly fossiliferous localities in the *Macroleura* band at Eden Park, a horizon characterised by an abundance of the large, thick-shelled brachiopod *M. densilineata*. At PL6615, dalmanitids (relative abundance 50%) are more abundant than proetids (relative abundance 21%), whereas at PL6614 the proetids are dominant (relative abundance 55%) over dalman-

itids (relative abundance 26%). The relative abundances of *garratti* and *williamsi* are similar at both localities (17–19% and 2% respectively).

The taphonomy and facies of *Dipleura garratti* differs markedly between PL6614 and PL6615. At PL6615, 87% are isolated tergites and the remainder are cephalia. With the exception of the cephalon of *Homalonotus williamsi* all other trilobites associated with *garratti* are represented by isolated tergites, with the proportion of broken specimens 16%. The lithology is best described as a bioclastic coquina in a siltstone matrix. Assignment to shallow taphofacies TII is in accord with Garratt's (1983) assignment of the brachiopod fauna to the shallow-water *Notoconchidium* Community (BA2). A moderate energy environment at depths around normal wave base is indicated. Slightly deeper conditions are indicated by the taphonomy and lithofacies at PL6614, where 21% of specimens of *garratti* are cephalia and 21% are cephalothoraxes. The proportion of broken specimens (9%) is lower than at PL6615. The lithology at PL6614 is a poorly bedded micaceous siltstone, and although bioclasts are extremely abundant they have not been winnowed to form a coquina. The preservation suggests an environment at depths below normal wave base.

Parahomalonotus Reed, 1918

Type species. *Homalonotus gervillei* De Verneuil, 1850. From the Pragian of France, Turkey, Spain, Morocco, Romania and Turkey, by original designation.

Other species included. *Parahomalonotus diablintianus* Morzadec, 1976, *Homalonotus vialai* Gosselet, 1912 (in Gosselet et al.), *P. sp. A* (= *P. gervillei* in Haas, 1968), *P. sp. B* (= *P. aff. gervillei* in Wenndorf, 1990).

Other species tentatively included. *Digonus* sp. cf. E in Morzadec, 1986.

Range. Lower Devonian.

Revised diagnosis. Glabella moderately to strongly convex (tr. sect.) and narrow, with length 1.2–1.6 times width. Axial furrows moderately to deeply impressed. Lobation distinct, S1–S3 moderately to deeply impressed. Pygidial axis narrow (0.35–0.4 times pygidial width anteriorly), weakly tapering (~25–30°), with moderate to strong convexity independent of the pleural convexity, raised posteriorly, continuous with wide postaxial ridge reaching posterior margin, pygidial tip with small point or short slender spine.

Discussion. The restricted diagnosis of *Parahomalonotus* defines a tight group distinct from *Wenndorfia*, to which many species previously assigned to *Parahomalonotus* have been assigned. Species assigned to *Parahomalonotus* also share weak glabella tapering (0–18°), a preglabellar field of moderate (0.2) to short (0.05) length, eyes placed posteriorly (opposite 0.35–0.5 cranial length), subparallel to moderately convergent anterior branches of facial suture, a transverse rostral suture, an obtusely angled (130–150°) to rounded pygidial tip and equally well defined axial rings and pleural ribs.

Pygidial morphology of *Parahomalonotus* is distinct from that of *Wenndorfia* and is conservative, with the exception of

P. diablantianus in which pygidial ring and pleural furrows are relatively shallow and the pygidial outline distinctly rounded. In cephalic features, the younger late Pragian-Emsian forms (*P. sp. A*, *P. gervillei*) differ from earlier species in their stronger glabellar convexity and lobation, and greatly reduced preglabellar fields. Of the earlier taxa, *P. vialai* shows the closest affinities with the type species and represents an intermediate morphology in which glabellar furrows and lobation are more moderately expressed.

To the species *Parahomalonotus sp. A* illustrated by Haas (1968: pl. 30 figs 1–4 as *P. gervillei*) from the Emsian of Turkey can be added at least one of the cranidia (pl. 29 fig. 26) described as *Dipleura fornix*, differing from other specimens of *fornix* in having a transverse glabellar anterior margin and straight rather than concave glabellar sides.

Trimerus Green, 1832

Type species. *Trimerus delphinocephalus* Green, 1832 from the Wenlock Rochester Shale, New York State, by monotypy.

Subgenera included. *Trimerus* (*Trimerus*) Green, 1832, *T. (Ramiotis)* subgen. nov., *T. (Edgillia)* subgen. nov.

Range. Llandovery–Lochkovian.

Revised diagnosis. Cephalon triangular to rounded pentagonal in outline, length 0.6–0.7 times width, anterior margin entire, trilobed or tricusped. Preglabellar field of moderate length to very long, 0.16–0.35 times cranidial length, flat or weakly concave (tr.) medially. Glabella generally with distinct lobation and median indentation of anterior margin. Eyes placed forwardly, with midline of palpebral lobes opposite 0.5–0.75 glabellar length (0.38–0.5 cranidial length) and medially on genae (δ - δ 1.3–1.7 times preoccipital glabellar width). Anterior branch of facial suture more or less straight and moderately convergent (45 – 60°) between eye and a point opposite midlength of preglabellar field. Rostral suture on dorsal surface, transverse or arching forwards evenly or with a median angle. Paraglabellar areas large. Ventral surface of rostral plate flat or weakly convex, without process. Thoracic axial furrows poorly defined. Pygidium with axis of moderate width (0.3–0.6 times pygidial width), not reaching posterior margin, axial furrows moderately impressed, axial ring and pleural furrows distinct but of variable depth, 6–12 rings, 5–10 ribs.

Discussion. The revised diagnosis incorporates and quantifies most features listed in more recent diagnoses of *Trimerus*. New characters include the relatively forward position of the eye, the straight course of the anterior branch of the facial suture, and the moderate axial width. Early diagnoses, such as Salter's (1865), predominantly list characters of a very general nature.

Three species groups are recognised in this work and defined as the subgenera *Trimerus* (*Trimerus*), *T. (Ramiotis)* and *T. (Edgillia)*. Previous diagnoses of *Trimerus* emphasise the well-defined glabellar lobation, triangular pygidial outline and acuminate pygidial tip (i.e. a mucro) exhibited by the type species and shared with closely related species including *T. (T.) cylindricus*, *T. (T.) vomer* (Chapman, 1912) and *T. (T.) johannis*. These features and a suite of other distinctive glabellar features are considered here to be diagnostic only of the typical

subgenus *T. (Trimerus)*. The forwardly arcuate course of the rostral suture and the short length (sag.) of the dorsal section of the rostral plate noted in previous diagnoses of *Trimerus* (Tomczykowa, 1975, Thomas *in* Curtis and Lane, 1998) is considered here to be only of specific significance for *T. (T.) delphinocephalus*.

A second group comprising other Silurian species of *Trimerus* can be recognised, and is described in this work as *T. (Ramiotis)*. Members of this group lack the produced pygidial tip and distinctive glabellar features of *T. (Trimerus)*. The group is typified by a new upper Llandovery species from Victoria, *T. (R.) rickardsi*. The species assigned to this group share a suite of characters including less acute to obtusely angled pygidial tips lacking a mucro, and an elongate, weakly tapering, more or less straight-sided glabella with weakly defined lobation. Tomczykowa (1975) included a slight degree of tapering of the glabella in her diagnosis of *Trimerus*, but this character is peculiar to *T. (Ramiotis)*. The degree of glabellar tapering in *Trimerus* varies between the strongly tapered ($\sim 55^\circ$) and posteriorly expanded morphologies of *T. (Trimerus)*, moderately tapered trapezoid morphologies of *T. (Ramiotis)*, and very weakly tapered ($<15^\circ$) subquadrate morphologies of *T. (Edgillia)*, the latter erected in this work for a group of Upper Silurian–Lower Devonian species. *T. (Ramiotis)* is further distinguished from *T. (Trimerus)* by a tendency towards a shorter preglabellar field, shorter pygidial proportions and more weakly defined pygidial segmentation. *Trimerus* (*Edgillia*) can be distinguished from the Silurian subgenera by a distinctive morphology typified by the Victorian *T. (E.) kinglakensis* (Gill, 1949). The species assigned share a very weakly tapered, subquadrate glabellar outline, weakly defined glabellar lobation, and lack the raised postaxial ridge present on most Silurian representatives of *Trimerus*.

Sdzuy (1959) considered *Trimerus* to comprise also the subgenus *Dipleura*. The revised diagnosis of *Dipleura* is in accord with Tomczykowa (1975) and Wendorf (1990) in recognising *Dipleura* and *Trimerus* as independent genera. Sdzuy's diagnosis of *T. (Trimerus)* emphasises differences from *Dipleura*, listing the longer cephalic proportions, a more tapering glabella, distinct glabellar lobation and paraglabellar areas, a forwardly convex rostral suture, an acuminate pygidial tip, and more distinct pygidial segmentation. Diagnoses of *Trimerus* by Thomas (*in* Curtis and Lane, 1998) and Tomczykowa (1975) closely follow Sdzuy's brief subgeneric diagnosis, but incorporate only some of the features listed by him. Importantly, both Thomas and Tomczykowa omitted the morphology of the rostral plate as a diagnostic character. Holloway and Neil (1982) suggested the significance of homalonotid coaptive morphologies, and in accord with this view the absence of a rostral process is reinstated in the diagnosis. In emphasising this feature and in the presence of other differences, a number of Lower Devonian species previously assigned to *Trimerus* are excluded, including *Homalonotus noticus* from South America and South Africa), *Burmeisteria (Digonus) accraensis* from Ghana and *Trimerus novus* Tomczykowa, 1975 from Poland.

Edgecombe and Fortey (2000) reassigned *Homalonotus lineares* Salter, 1861 from the Pířdól of Bolivia to *Trimerus*. The species exhibits a number of features that are not com-

patible with this assignment. The axial ring count (14–16) is higher than any species assigned to *Trimerus* (ranging 6–12), the width of the axis (up to 0.7 width) is greater than in any species assigned to *Trimerus* (ranging 0.3–0.6 width), the pygidium is longer (length/width ratio 1.1–1.2) than all species of *Trimerus* (length/width ranging 0.6–1.0) except for *T. (Trimerus) cylindricus* Salter (1865), and the cephalic proportions are longer (“transverse width slightly exceeding length”: Edgcombe and Fortey, 2000: 332) than any species of *Trimerus* (length/width ranging 0.6–0.7), complementing its elongate pygidial proportions. These features are more compatible with assignment to *Burmeisteria*. The type species, *B. herschelii* exhibits comparably high pygidial segmentation (16–17 axial rings, 9–11 pleural ribs), elongate pygidial proportions and a wide pygidial axis. Although the course of the rostral suture and the morphology of the rostral plate (including the presence of a ventral process) for *B. lineares* remains uncertain, there is a suggestion of moderate convexity of the rostral plate in one of the cranidia illustrated by Edgcombe and Fortey (2000: pl. 2 fig. 16).

In addition to the several species reassigned to *Burmeisteria* and *Digonus* (discussed above), a considerable number of species assigned to *Trimerus* by Tomczykowa (1975) and Wenndorf (1990) are assigned to other genera. *T. lilydalensis* is assigned below to *Wenndorfla*. Pygidia from the upper Pragian of Morocco, identified by Schraut (2000) as *T. sp. cf. crassicauda* are too fragmentary for confident assignment to *Trimerus*, although the shallower axial ring and pleural furrows preclude assignment to the German species. The relationships of a number of poorly documented taxa previously assigned to *Trimerus* are uncertain, including *Homalonotus acuminatus* Tromelin and Lebesconte, 1876 and the French *H. leheri* Barrois, 1886.

Trimerus (Trimerus) Green, 1832

Type species. *Trimerus delphinocephalus* Green, 1832, from the Wenlock Rochester Shale, New York State, by monotypy.

Other species included. *Homalonotus (Trimerus) cylindricus* Salter, 1865, *T. (T.) flexuosus* Benedetto and Martel (in Baldi et al., 1976), *H. harrisoni* McCoy, 1876, *H. (T.) johannis* Salter, 1865, *H. vomer* Chapman, 1912, *T. (T.) sp. A* in Alberti (1970), *T. sp. in* Owens (1994).

Range. Wenlock-Ludlow, Přídolí?

Diagnosis. Glabella moderately to strongly expanded across L1–L1 (tr.), strongly raised, markedly narrower (tr.) anteriorly than posteriorly (sides tapering at 33–55°, width opposite S3 less than 0.65 times L1–L1). S1 moderately to strongly expressed, S2 and S3 distinct or fused with S1 to form a shallow exsagittal depression. L1 and L2 with low ovoid swellings. Sagittal ridge of glabella well defined. Preglabellar field long to very long (0.22–0.35 times cranial length), distinctly concave (tr. sect.). Pygidial length equal to or greater than width. Pygidial ring furrows and pleural furrows of similar depth, 10–12 axial rings, 7–9 ribs. Pygidium with acutely produced tip or with short, spine-like process.

Discussion. The type species *Trimerus delphinocephalus* belongs to a distinct species group within *Trimerus*, restricted in distribution to the mid Wenlock-lower Ludlow interval. The

group is easily recognised in having distinctive glabellar features, particularly the glabella with an outline markedly expanded across L1–L1 (tr.), raised profile, distinct lobation, swellings on L1 and L2, and the sagittal ridge. In comparison to other members of *Trimerus*, these species also have more elongate preglabellar fields, more elongate and more highly segmented pygidia, and bear a short spine or acute process on the pygidial terminus. The species assigned are easily distinguished from other *Trimerus*, in which the characters listed are only occasionally or weakly expressed.

The characteristic cephalic features of *Trimerus (Trimerus)* are expressed most strongly in *T. (T.) johannis* from the upper Wenlock of England and *T. (T.) vomer* from the basal Ludlow in Victoria. These species are interpreted as the most highly derived of those assigned. Populations of *T. (T.) delphinocephalus* show wide morphological variability and the cephalic features characteristic of the subgenus are variably expressed, although they are clearly present in specimens figured by Whittington (1993: figs 1, 2). Pygidia of *delphinocephalus* differ from those of *johannis* and *vomer* in having shallower ring furrows and pleural furrows, and a short spine-like process posteriorly. In outline, the depth of the pygidial furrowing and presence of a posterior spine a single pygidium documented from the Upper Silurian of Morocco (Alberti, 1970, Schraut, 2000) closely resembles pygidia of *delphinocephalus* and is also assigned to the subgenus.

Trimerus (Trimerus) flexuosus from the Wenlock-Ludlow? of Argentina is poorly known but is clearly attributable to *T. (Trimerus)*. Benedetto and Martel (in Baldi et al., 1976) describe the species as having a raised glabella with distinct S1–S3, subcircular-ovate swellings on L1, and strongly defined paraglabellar areas, features characteristic of the subgenus. The pygidium closely resembles that of *T. (T.) sp. (in* Alberti, 1970) from Morocco in outline, in the depth of the pygidial furrowing and in the presence of a posterior spine. The rostral suture is convex, as in the type species.

An incomplete cranidium figured as *Trimerus sp.* from the upper Wenlock Brinkmarsh Beds of England (Owens, 1994: pl. 2 fig. J) can be assigned to *T. (Trimerus)*. In outline and height the glabella is not unlike that of *T. (T.) johannis* from the nearby area, to which it may belong.

The anterior margin of the cephalon is variably expressed in *Trimerus (Trimerus)*. In *T. (T.) vomer*, the angle of convergence of the sides of the cephalon increases abruptly opposite the antero-lateral corners of the cranidium, giving the cephalon an irregular pentagonal outline. In *T. (T.) johannis* (and possibly *T. (T.) flexuosus*) the anterior margin of the cephalon is tricusate, with the sides of the cephalon invaginated opposite the connective suture. The weakly trilobate anterior margin of the cephalon of *T. (T.) delphinocephalus* is intermediate between these morphologies.

Trimerus (Trimerus) harrisoni (McCoy, 1876)

Figures 5B, 19.7, 19.9, 19.11

Homalonotus harrisoni McCoy, 1876: 19, pl. 23 fig. 11.

Trimerus harrisoni.—Gill, 1949: 65, text-fig. 1A.—Sandford, 2000: 189, figs. 17A–E.

Remarks. I recently provided a comprehensive synonymy, revised diagnosis and description for *Trimerus* (*Trimerus*) *harrisoni* (see Sandford, 2000). No new material has been obtained. Poor preservation of all known cranidia obscures many features of the cephalon pertinent to its subgeneric assignment. The glabella is not strongly raised, although this is true also of the type species *Trimerus* (*Trimerus*) *delphinocephalus*. The glabella tapers very strongly forwards, although whether bell shaped or trapezoid in outline is not clear as the best-preserved specimen is somewhat crushed. The poorly known pygidia of *harrisoni* resemble those of the type species in the depth and relative depth of the pleural and ring furrows, although differ in having a prominent postaxial ridge and possibly in lacking a posterior spine. In respect to these latter differences, the pygidial morphology of *harrisoni* is not incompatible with *T. (Ramiotis)*. However, the strong tapering of the glabella and exceptional length of the preglabellar field are emphasised here in assigning the species to *T. (Trimerus)*.

Trimerus* (*Trimerus*) *vomer (Chapman, 1912)

Figure 15

Homalonotus vomer Chapman, 1912: 298, pl. 62 figs 2, 3, pl. 63 fig. 2, non pl. 63 fig. 1 (= *Trimerus* (*Ramiotis*) *otisi* sp. nov.)

Homalonotus (*Trimerus*) *vomer*.—Reed, 1918: 323.

Trimerus vomer.—Gill, 1949: 65, text-fig. 1C non 1B (= *Trimerus* (*Ramiotis*) *otisi* sp. nov.).—Tomczykowa, 1975: 11. —Wenndorff, 1990: 16. —Schraut, 2000: 383.

Type material. Holotype NMV P12301 (cephalon and displaced thorax, figured Chapman, 1912, pl. 62 fig. 1, 2, Gill, 1949a, text-fig. 1C, Fig. 15.4 herein) from “Wandong”, Victoria. Paratype NMV P12302 (thoracopygon, figured Chapman, 1912, pl. 63 fig. 2 from “Wandong”). Paratype NMV P12303 (cephalon, figured Chapman, 1912, pl. 63 fig. 1, Gill, 1949a, text-fig. 1B) from “Wandong”. For localities see Fig. 11.

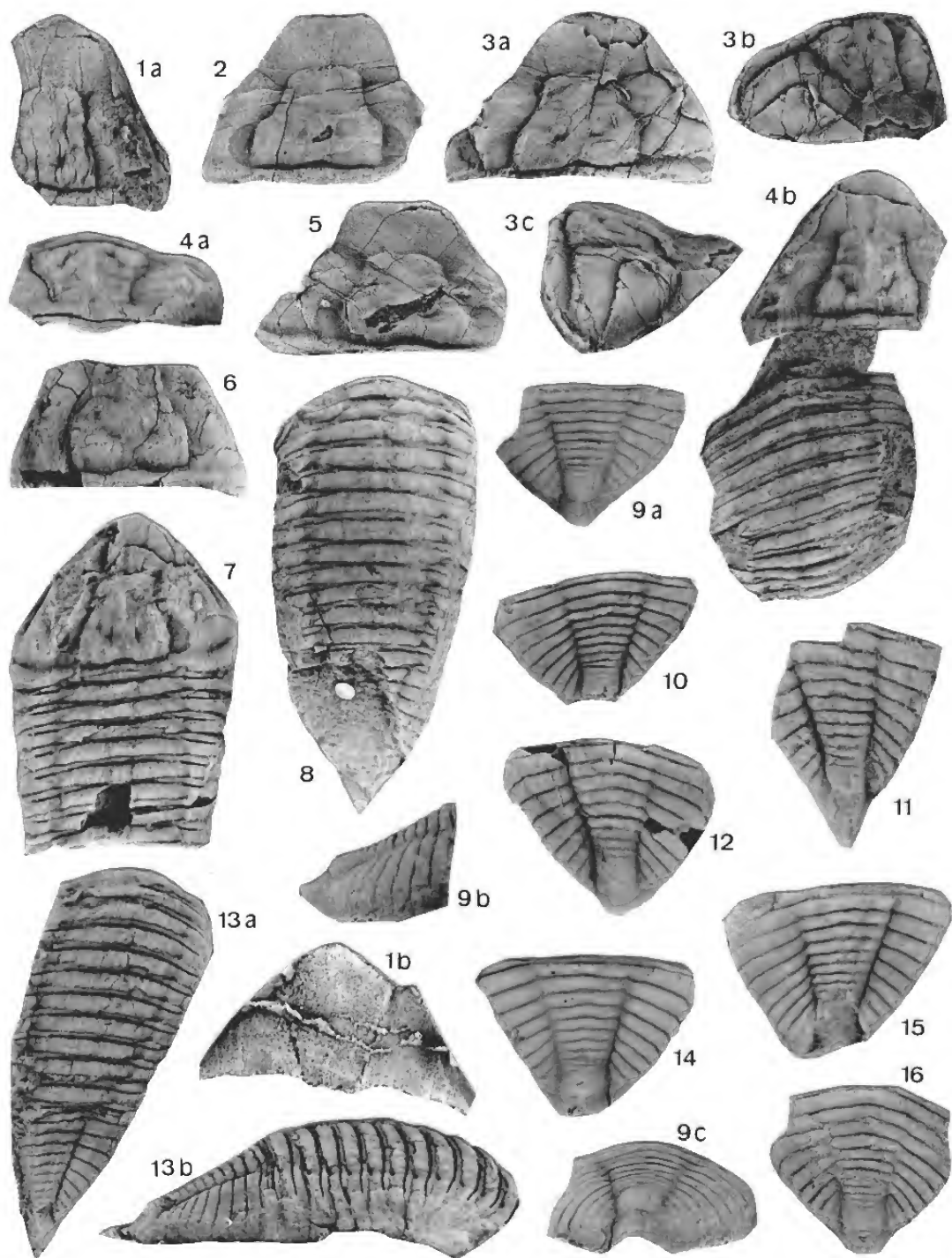
Registered material. 55 specimens. NMV P455, NMV P529, NMV P16415, NMV P136623–P136627, NMV P136629–P136633, NMV P137158, NMV P137291, NMV P137910 from “Wandong”. NMV P136612–P136622, NMV P136628, NMV P136680, NMV P137120, P137121, NMV P137126–P137137 from PL286, Williams locality F22, Kilmore East, Victoria. NMV P136634–P136636 from “Kilmore East–Sunday Creek Road”, Kilmore East. NMV P136637 from “Langford Park”, Kilmore East. NMV P136846, NMV P137887 from “Kilmore”, Victoria. NMV P137122–P137124, NMV P137144, NMV P138649 from “Kilmore–Wandong”. NMV P137144 from PL868, Kilmore East. Yan Yean Formation. NMV P136638 from “Heathcote”, Victoria. For localities see Fig. 11.

Revised diagnosis. Cranial width 1.5 times length. Glabella strongly raised, length equal to width, strongly bell shaped in outline, much narrower anteriorly than posteriorly, anterior margin well defined, with deep medial indentation. S1–S3 distinct, S1 with deeply impressed apodeme at adaxial end. Paraglabellar area very strongly defined. Preglabellar field very long, 0.3 times cranial length, weakly concave (tr. sect.). Palpebral lobes placed opposite 0.5 cranial length (0.7 glabellar length). Weak but distinct eye ridges. Anterior branches of the facial suture straight, converging at about 55° to a point opposite midlength of preglabellar field. Rostral suture transverse. Dorsal section of rostral plate triangular, long, 0.1

cephalic length. Ventral section of rostral plate elongate, width 0.85 times length, connective sutures straight and converging posteriorly at 35°. Pygidium triangular, length equalling width, with broad based, acutely pointed tip. Axial furrows moderately to deeply impressed. Axial width (measured across second ring) 0.37 times pygidial width. Axis raised, markedly swollen posteriorly. Wide postaxial ridge. 10–12 axial rings. 8 pleural ribs with ninth rib reduced or absent. Pygidial pleural and ring furrows deep, of equal depth. Rib-ring medial offset at fifth rib.

Description. Exoskeleton maximum length estimated 12 cm long. Exoskeleton granulate, more densely in the alae, finely tuberculate thoracic segments.

Cephalon triangular, length 0.8 width, in transverse and sagittal section posteriorly convex, anteriorly concave, lateral margins converging at 70–80°, genal angles and anterior tip rounded. Glabella 0.6 cephalic length, strongly bell shaped, narrowing markedly opposite palpebral area, posterior width equal to length and twice anterior width, in section (tr., sag.) weakly convex posteriorly, less so anteriorly. Occipital ring transverse, lower than glabella, 0.1 glabellar length, slightly wider at medial apex, in transverse section arched at medial apex, sloping at a uniform gradient abaxially, not interrupted by axial furrow and thus continuous with posterior border. Occipital furrow deeply impressed, strongly deflected forwards medially and less so abaxially, wider at medial apex. S1 a wide shallow furrow directed inwards backwards between 0.2 and 0.4 preoccipital glabellar width, deeper at extremities. L1 weakly defined as an independently convex, triangular lobe, widest abaxially, maximum exsagittal length 0.3 glabellar length. S2 and S3 weakly defined as wide shallow depressions not connected with axial furrows. L2 and L3 undefined. Frontal lobe impressed medially by a short (sag.) wide notch. Axial furrow developed posteriorly as large semicircular alae as long as and placed opposite L1. Anteriorly axial furrow very wide, deepening opposite antero-lateral corner of glabella. Preglabellar furrow indistinct, defined as a change in height from the frontal lobe to the frontal area. Frontal area long (sag.), 0.4 glabellar length. Medial area increasingly concave anteriorly, margins increasingly convex posteriorly in transverse section. Genae inflated. Fixigenae wide (tr.), approximately 0.5 preoccipital glabellar width at midline. Palpebral area wide and convex (tr.), palpebral lobe inclined at 45°, semicircular, 0.25 glabellar length (sag.), placed anterior of and adjacent to glabellar transverse midline, weak eye-ridge directed inwards forwards to a point opposite S3. Anterior to palpebral area fixigenae sloping down to frontal area, not extending anteriorly as far as glabella. Posterior to palpebral lobe fixigenae wide (exsag.), 0.33 glabellar length, narrowing abaxially, strongly convex. Posterior border furrow wide, shallowing and curving forwards abaxially. Posterior border lower than genal area, increasingly convex (exsag.) and widening to twice occipital ring width (sag.) abaxially. Genal angle broadly rounded. Anterior facial suture converging forwards at about 60°, meeting connective suture very close to margin at a point opposite 2/3 sagittal length of frontal area (measured from glabella). Connective sutures short on dorsal surface, diverging forwards at 90°. Rostral suture transverse. Posterior branch of facial suture transverse adaxially, curving backwards abaxially, crossing margin just anterior of genal angle. Librigenae triangular, convex, steep. Eye small, raised above genal surface. Lateral border furrow defined as an angular change in slope, less distinct toward genal angle. Lateral border narrowing anteriorly by a factor of four from genal angle, flat and horizontal. Lateral border and furrow indistinct anterior to genae. Anterior facial sutures converging at 60°, close to margin and curving inwards anteriorly, meeting connective suture on a transverse line 0.3 sagittal length of frontal area from anterior tip. Connective suture short on dorsal surface, diverging at 90°. Ventral portion of



rostral plate flat, elongate pentangular, long (sag.), 0.4 cranial length (extending to anterior margin of glabella), maximum width 0.8 length, placed at 0.75 rostral length. Connective sutures straight, converging posteriorly at 35°, posterior margin transverse, 0.4 maximum width. Dorsal portion of rostral plate triangular to weakly crescentic, flat, very short (sag.) length 0.2 width between posterolateral corners and 0.2 ventral length. Anterior margin straight abaxially, each side converging at 110°, medially rounded. Rostral suture convergent at 170° laterally (to one third maximum width), transverse medially. Connective sutures short (exsag.) apparently marginal between posterolateral corners of dorsal portion and anterolateral corners of ventral portion. Doubleure posterior margin transverse, as wide as rostral plate adjacent to connective suture but narrowing adaxially. Adjacent to lateral margin doubleure concave in section such that it closely parallels the dorsal exoskeleton.

Thorax 11 segments. Axis cigar shaped, weakly convex (tr.), wide, 0.7 (max.) thoracic width in dorsal view. Pleural field narrow in dorsal view, 0.15 thoracic width, convex (tr.), flexed to subvertical, twice as long abaxial of flexure than adaxial. Axial rings convex (sag.), transverse, wider medially than abaxially. Pleural furrow continues onto rings, deep slot-like, defining anterior band wider abaxially. Axis distinguished from pleural field by independent convexity and by a depressed area in the posterior edge of the pleurae. Pleural furrow divides narrow anterior band from posterior band twice as wide, shallows towards tip. Abaxially of flexure pleurae widen slightly, almost wholly occupied by articulating facet, which has a rounded tip.

Pygidial proportions as for cephalon. Trilobation distinct. Anteriorly axis as wide as pleurae, tapering uniformly, 0.8 pygidial length, in transverse section axis weakly convex anteriorly to strongly convex posteriorly. In sagittal section axis concave anteriorly, posteriorly with long prominent swelling and strongly concave. 9–10 distinct rings, swelling 0.25 axial length and very feintly ringed. Axial rings very weakly convex (sag.) and weakly convex-forwards. Anterior ring furrow higher than others, second ring with pseudo-articulating half-ring. Rings 1–7 of uniform width, posterior rings (8+) as narrow ridges. Posterior of axis border strongly arched (tr. sect.) and high. Axial furrow shallow and wide. Pleural field uniformly convex. Pleural furrows distinct. 9 ribs, wider than rings, and widening abaxially, flat (exsag.). Interpleural furrows not distinct. Border narrow, concave, widening posteriorly.

Remarks. Many of the characters listed as diagnostic of *Trimerus* (*Trimerus*) *vomer* are strongly expressed in *T. (T.) vomer*, including the definition of S1 and L1 and L2 swellings, the paraglabellar area, the length of the preglabellar field and the bell-shape of the glabella. *T. (T.) vomer* also displays a number of unusual characters including distinct eye ridges and deep S1 apodemes, and further differs from other members of *Trimerus*

(*Trimerus*) in having a particularly long rostral plate (dorsally), and very forwardly placed eyes. The deep S1 apodemes are one of the most distinctive features of *vomer*. The orientation and position of these apodemes appears to be somewhat variable, however, being transverse on some specimens, diagonal on others, and sagittal on others. These differences may well be attributable to deformation, as is suggested by the correlation of glabellar proportions with apodeme orientation. Specimens with tectonically shortened glabellae (L:W~0.8) have transverse apodemes, those with tectonically elongated glabellae (L:W~1.1) have sagittally directed apodemes. The predeformational orientation was probably diagonal, as in the holotype.

Although with many unique characters, *Trimerus* (*Trimerus*) *vomer* is most closely comparable to *T. (T.) johannis* from the Wenlock of Wales. These species share a transverse rostral suture, a markedly raised and very strongly expanded (tr.) glabella (more exaggerated in *vomer*), very distinct and large paraglabellar areas and a distinctly concave preglabellar field. The deep ring furrows and pleural furrows, the strong swellings on the pygidial axis posteriorly (more prominent on *vomer*) and the acute process defining the pygidial tip distinguish *vomer* and *johannis* from other species of *T. (Trimerus)*. These two species differ in that *vomer* has more forwardly placed eyes, distinct eye ridges, a longer preglabellar field, an entire cephalic anterior margin, deep apodemes on S1 and distinct S2–S3 (fused to define a shallow exsagittal furrow in *johannis*).

As noted by Chapman (1912), *Trimerus* (*Trimerus*) *vomer* is also close to the type species, *T. (T.) delphinocephalus*. Feint eye ridges and very weak L1 apodemes have been observed (Whittington, 1993, fig. 2a) on *delphinocephalus*, and are comparable to those on *vomer* (Figs 15.3–15.4). The most conspicuous differences include the much wider pygidial axis, shallower pygidial furrows, the convex rostral suture, the angular (rather than straight) connective sutures, the low glabella and the less elongate pygidial outline of *delphinocephalus*.

The cephalon designated as paratype by Chapman and considered by him to be a juvenile form is not conspecific with the holotype. The specimen (NMV P12303, see Fig. 20.1) lacks the bell shaped glabellar outline and deep lateral glabellar furrows of *Trimerus* (*Trimerus*) *vomer*, further differing from it in having distinct subocular and sutural furrows. The specimen is assigned in this work to *T. (Ramotisi) otisi*. Aspects of Gill's

Figure 15. *Trimerus* (*Trimerus*) *vomer* (Chapman, 1912). 1a, NMV P136613, cephalon, dorsal view $\times 1.2$ (latex cast) from PL286. 1b, same, ventral view (doubleure) $\times 2.45$. 2, NMV P136619, cranium, dorsal view $\times 1.0$ (internal mould) from PL286. 3a, NMV P136622, cephalon, dorsal view $\times 1.15$ (internal mould) from PL286. 3b, same, oblique view $\times 1.35$. 3c, same, lateral view $\times 1.35$. 4a, holotype NMV P12301, cephalon and displaced, incomplete and partly enrolled thorax, anterior view of cephalon $\times 0.95$ (internal mould) from "Wandong". 4b, same, dorsal view of cephalon and thorax $\times 0.88$. 5, NMV P138649, cranium, dorsal view $\times 0.92$ (internal mould) from "Kilmore-Wandong". 6, NMV P136638, cephalon, dorsal view $\times 0.85$ (internal mould) from "Heathcote". 7, NMV P16415, cephalon and incomplete thorax, dorsal view $\times 1.0$ (internal mould) from "Wandong". 8, paratype NMV P12302, thoracopygon, dorsal view $\times 0.92$ (internal mould) from "Wandong". 9a, NMV P136625, pygidium, dorsal view $\times 0.85$ (internal mould) from "Wandong". 9b, same, lateral view $\times 1.05$. 9c, same, posterior view $\times 0.85$. 10, NMV P137291, pygidium, dorsal view $\times 1.1$ (internal mould) from "Wandong". 11, NMV P137158, pygidium, dorsal view $\times 1.5$ (internal mould) from "Wandong". 12, NMV P137124, pygidium, dorsal view $\times 1.3$ (internal mould) from "Kilmore-Wandong". 13a, NMV P455, thoracopygon, Odorsal view $\times 1.1$ (internal mould) from "Wandong". 13b, same, lateral view $\times 1.2$. 14, NMV P136637, pygidium, dorsal view $\times 1.05$ (internal mould) from "Langford Park homestead, Kilmore East". 15, NMV P136633, pygidium, dorsal view $\times 1.25$ (internal mould) from "Wandong". 16, NMV P137910, pygidium, dorsal view $\times 1.0$ (internal mould) from "Wandong".

(1949) redescription of *vomer* are clearly based on this paratype, notably the description of the axial and glabellar furrows as shallow and faint (respectively).

Documenting an increasingly distal eye position in a succession of Victorian homalonotids, Gill suggested a migration of the *Trimerus* eye through time. In addition to the problem that the width of the librigenae and eye position for *T. (Trimerus) vomer* is measured from the paratype cephalon of *T. (Ramiotis) otisi*, Gill's model is flawed firstly, in that only two of the species in Gill's model can be assigned to *Trimerus*, secondly, in that the relative stratigraphic positions of the species in Gill's model are incorrect.

Environmental notes. Although no complete exoskeletons are known from the population of *Trimerus (Trimerus) vomer*, the articulation ratio of the population as a whole is high ($Ar=28\%$). *T. (T.) vomer* occurs in a fine siltstone lithology at all of the few localities from which it is known. The holotype is a cephalon displaced from an articulated thorax (Fig. 15.4), interpreted as a moult assemblage. As for *T. (Edgillia) kinglakensis*, articulated thoracopygons, cephalothoraxes and partly disarticulated thoraxes are interpreted as exuvial configurations (taphofacies TIV). An outer shelf deep-water habitat below maximum storm wave base is suggested for *vomer*.

Trimerus (Edgillia) subgen. nov.

Type species. *Trimerus kinglakensis* Gill, 1949 from the Lochkovian Humevale Siltstone, central Victoria.

Other species included. *Trimerus (Trimerus) grandis* Benedetto and Martel (in Baldi et al., 1976), *T. (Edgillia) jelli* sp. nov., *Homalonotus (Trimerus) mongolicus* Tchernycheva, 1937, *H. vanuxemi* Hall, 1859.

Other species tentatively included. *Homalonotus major* Whitfield, 1881.

Range. Upper Silurian-Lower Devonian.

Derivation of name. For the late E. D. Gill, for his contribution to Victorian palaeontology.

Diagnosis. Glabella subquadrate, length about 1.0 times width, sides straight and weakly tapered (converging at around $15-20^\circ$), anterior margin transverse, well defined, S2 and S3 indistinct, S1 indistinct or weakly defined, not extending to axial furrows. Eye placed more or less opposite glabellar midlength. Hypostomal middle furrow with deep impressions abaxially. 10–14 pygidial axial rings. Pygidial postaxial ridge poorly defined. Ring furrows deep, pleural furrows shallow. Pygidial length 0.85–1.0 times width.

Discussion. Represented by a population sample of over 300 partly articulated exoskeletons, *Trimerus (Edgillia) kinglakensis* is undoubtedly the best represented species of *Trimerus* from the Přídolí-Lower Devonian interval. *T. (E.) kinglakensis* differs markedly from many earlier representatives of *Trimerus* in its glabellar morphology, principally in having a subquadrate outline and a raised but evenly-vaulted surface. Species assigned here to *T. (Ramiotis)* differs in having a more strongly tapered and generally more elongate glabellar outline, with many exhibiting weak glabellar lobation and rounded anterior glabellar margins and pygidia with raised

postaxial ridges. The glabellar outline strongly expanded across L1-L1 (tr.), distinct glabellar lobation, paraglabellar areas, and the presence of a glabellar longitudinal ridge and glabellar antero-median indentation in *T. (Trimerus)* distinguishes *kinglakensis* from that group. The morphology exhibited by *kinglakensis* is shared with several poorly known Upper Silurian-Lower Devonian taxa and defines a species group for which *T. (Edgillia)* is established.

Homalonotus vanuxemi from North America is roughly contemporary with *Trimerus (Edgillia) kinglakensis*, occurring in Lower Devonian strata of New York State. The species was originally described from its thorax and pygidium (Hall, 1859). The later documentation of the cranium (Hall and Clarke, 1888: p. 11, plate 5b, Williams and Breger, 1916: plate 22, figs 12, 21, Shimer and Shrock, 1944: plate 272, fig. 32) demonstrates a cephalic morphology closely comparable with *kinglakensis*. In particular, the straight sides, transverse anterior margin and weakly tapered outline and proportions of the glabella of *vanuxemi* are almost identical to the Victorian species. With respect to the morphology of the preglabellar field, the illustrations of the cranium by Hall and Clarke and Shimer and Shrock are not in close agreement. Hall and Clarke noted an exceptionally long preglabellar field and a transverse rostral suture, although their observations were based on a single fragment. Shimer and Shrock illustrated a complete cranium with a somewhat shorter preglabellar field, and although the rostral suture is not clearly depicted it appears forwardly convex in outline. In these respects the cephalon illustrated by Shimer and Shrock is very close to *kinglakensis* and supports assignment of *vanuxemi* to *T. (Edgillia)*. The pygidia of these two species also share a relatively high degree of segmentation and both lack a raised postaxial ridge. The relative depth of the pygidial pleural furrows of *vanuxemi* is difficult to ascertain from the illustrations available. However, Hall and Clarke's illustration of a large specimen in lateral view (Hall and Clarke: pl. 5b fig. 2) suggests shallower pleural furrows than the ring furrows, as in *kinglakensis*.

Trimerus (Trimerus) grandis from the Upper Silurian-Lower Devonian of Argentina was described by Benedetto and Martel in Baldi et al. (1976) from a single specimen. Assignment of this species to *T. (Edgillia)* is supported by the raised, evenly vaulted glabellar profile, the subquadrate glabellar outline, the poorly defined glabellar lobation, and the relative shallowness of the pygidial pleural furrows relative to the ring furrows. The higher degree of pygidial segmentation (11–12 axial rings) is in accord with assignment to *T. (Edgillia)*.

A new species represented almost entirely by fragmented tergites from the Lochkovian of Victoria can also be assigned to *Trimerus (Edgillia)*. The material available is closely comparable to *T. (E.) kinglakensis* and *T. (E.) vanuxemi* and is described in this work as *T. (E.) jelli*. There are few other homalonotids recorded from the Lower Devonian that can be confidently assigned to *T. (Edgillia)*. *Homalonotus major* was described from a single, incomplete but very large thoracopygon. Whitfield (1881) estimated the specimen to represent an individual 15.5 inches (31 cm) and in its very large size the species is comparable to *kinglakensis*, *vanuxemi* and *T. (E.) grandis*. The depth of the axial ring and pleural furrows of

major and *kinglakensis* are comparable, although those of *major* do not appear to shallow abaxially. The specimen has 10 axial rings, although the posterior part of the pygidium is broken off and whether there were further rings or a postaxial ridge cannot be determined. On these few features the species is only doubtfully assigned to *Edgillia*.

Gill (1949) considered *Trimerus* (*Edgillia*) *kinglakensis* to be most closely related to, and directly descended from, the earliest Ludlow *T. (T.) vomer*. Gill constructed his phylogeny erroneously considering these species to be much closer in age than they actually are. Redescription of both *vomer* and *kinglakensis* shows that these species are not closely related. *T. (T.) vomer* is a highly derived species and *kinglakensis* exhibits none of its characteristic features. With respect to the presumably ancestral *T. (Ramiothis)*, morphoclines of increasing glabellar complexity defining *T. (Trimerus)* are contrary to morphoclines of decreasing glabellar complexity characterising *T. (Edgillia)* and suggest independent derivation of these subgenera.

Trimerus (*Edgillia*) *kinglakensis* (Gill, 1949)

Figures 5A, 5D, 16, 17.1–17.7

Homalonotus sp.—Gill, 1947: 13.

Trimerus kinglakensis Gill, 1949: 67, pl. 8 figs 1–3, pl. 9 figs 3, 5–6, text-fig. 1E.—Williams, 1964: table 1.—Wenndorf, 1990: 16.—Jell, 1992: 11, text-fig. 1B.—Schraut, 2000: 382.

Type material. Holotype NMV P14580 (cephalon, figured Gill, 1949: pl. 8 figs 1, 2, pl. 9 fig. 3, text-fig. 1E, Fig. 16.12 herein, counterpart previously registered NMV P14581) from PL252, Williams locality W3, Middendorps Quarry, Kinglake West, Victoria. Paratype NMV P14582 (thoracopygon, figured Gill, 1949: pl. 8 fig. 3, counterpart previously registered NMV P14583) from PL252. For locality see Fig. 11.

Previously figured material. NMV P14584 (thoracopygon, figured Gill, 1949: pl. 9 fig. 5), NMV P14585 (pygidium, figured Gill, 1949: pl. 9 fig. 6, counterpart previously registered NMV P14586) from PL252.

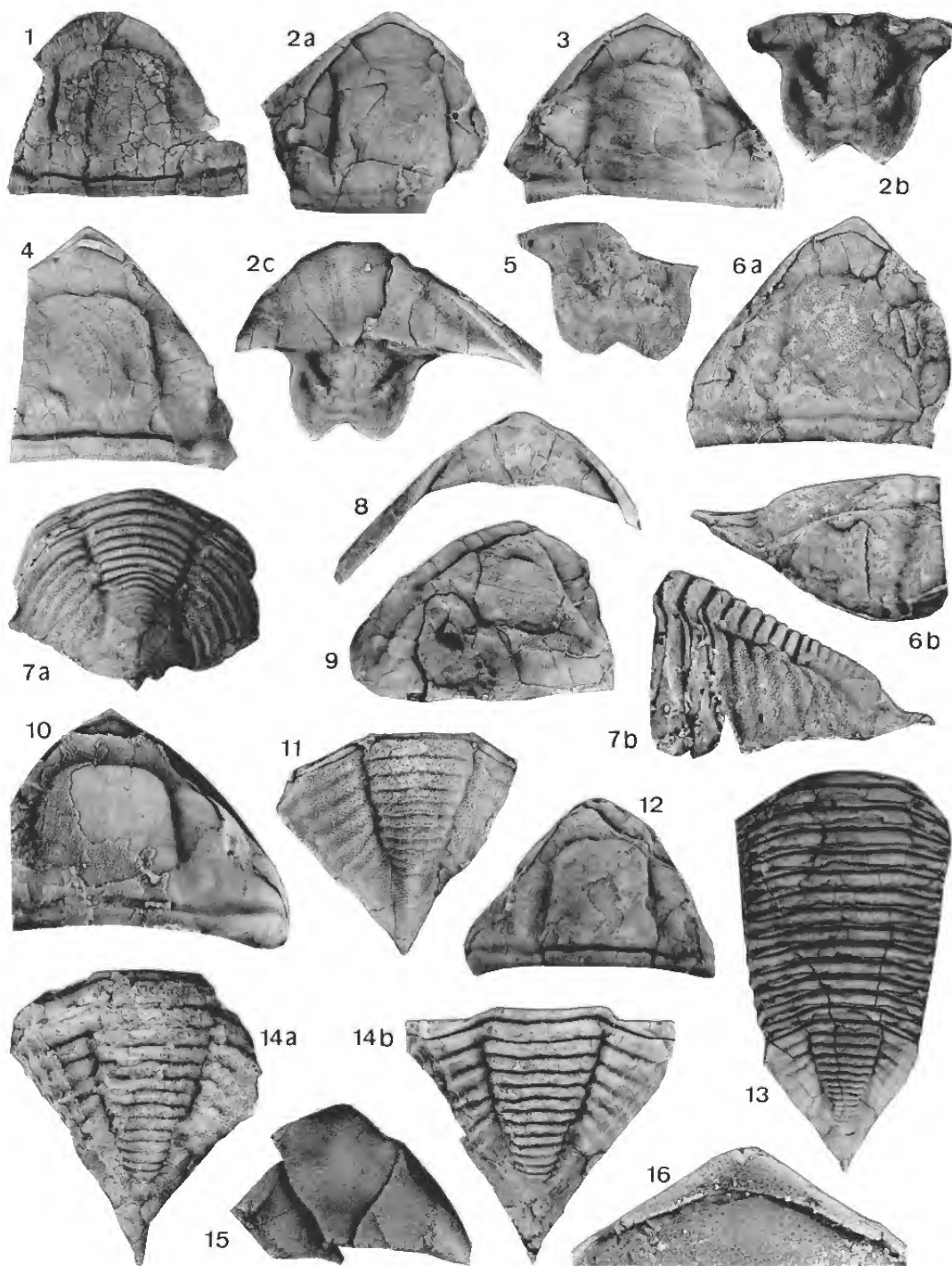
Registered material. 307 specimens: 2 dorsal exoskeletons, 22 articulated thorax-pygidia with displaced cephalae, 29 articulated thoraxes with displaced cephalae, 12 articulated thorax-pygidia with inverted cephalae, 3 articulated thoraxes with inverted cephalae, 3 articulated thoraxes with displaced cephalae and pygidia, 110 articulated or partly disarticulated thoraxes with attached pygidia, 10 articulated or partly disarticulated thoraxes with displaced pygidia, 32 cephalae, 4 cranidia, 1 librigena, 30 articulated or partly disarticulated thoraxes, 50 pygidia. NMV P149634, P149635, NMV P305248–P305545 from PL252. NMV P305546 from “Kinglake”, Victoria. NMV P305547 from “King Parrot Creek”, Kinglake West. NMV P304849 from PL6640, Garratt locality M8, Heathcote Junction. NMV P304850 from PL6641, Williams locality G96, Clonbinane. NMV P304853, P304854? from PL6645, Williams locality W47, Humevale. NMV P304852? from PL6648, Humevale. NMV P304857? from PL6659, Williams locality W8, Kinglake West. NMV P304856 from PL6660, Humevale. Unregistered specimen from PL229, Williams locality W7, Collins Quarry, Kinglake West. For localities see Fig. 11. NMV P305548–P305550 from “Christmas Hills”, Victoria (probably in the vicinity of PL261). For locality see Jell and Holloway, 1983: fig. 1. NMV P305551, P305552 from old Scoresby Brick Pit, Wantirna South, Victoria.

Stratigraphic distribution. Humevale Siltstone (from basal horizons at the old Scoresby Brick Pit to the Collins Quarry Sandstone Member at the top of the unit), upper *Notoparmella plentiensis*–*Boucotia janae*–*Boucotia australis* assemblage zones, Přídolí–Lochkovian.

Revised diagnosis. Cranidial width 1.5 times length. Glabella trapezoid, length more or less equal to width, sides straight, converging at about 15°, anterior margin well defined. Proximal section of S1 moderately impressed, directed diagonally, glabellar lobation otherwise poorly defined. Preglabellar field 0.2 times cranidial length. Palpebral lobes placed opposite glabellar midlength/0.4 cranidial length and remote (δ – δ 1.55 times preoccipital glabellar width). Anterior branches of facial suture angular, parallel to axial furrows for a short distance posteriorly, converging at about 80° anteriorly. Librigenal border furrow weakly defined. Course of rostral suture angular, defining an obtuse angle of about 140°, dorsal section of rostral plate boomerang-shaped. Hypostome with middle furrow very deep, posterior border with wide, short triangular lobes (length 0.1 times hypostomal length) and deep, angular medial notch. Pygidium triangular, length 0.95 times width, with long pointed tip, sides straight, converging at about 75°. Axial furrows moderately impressed opposite first ring, deep posteriorly. Axial width 0.45 times pygidial width. 13–14 axial rings. 7 pleural ribs, rib-ring medially offset at third rib, pleural furrows markedly shallowing abaxially. Dorsal exoskeleton very strongly pitted.

Description. Exoskeleton large, maximum size estimated 25 cm (from NMV P305258), occipital/pygidial convexity (tr.) moderate. Pygidial and librigenal doublure and hypostome finely ornamented with short ridges.

Cephalon with rounded triangular outline with weakly convex sides, converging forwards at about 70° opposite genal field and at 115° opposite rostral plate, length 0.66 times width. Glabellar length about equal to width (although difficult to quantify due to the poor definition of the axial furrows posteriorly), width about 0.5 times cranidial width, sides straight to weakly convex, length 0.8 times cranidial length, anterior margin transverse, medial indentation moderately impressed to absent. Glabellar lobation very weakly defined, generally only the proximal part of S1 distinct, S2 distinct only on smallest specimens (e.g. NMV P305272, see Fig. 16.10). S3 indistinct. Occipital ring 0.1 times cranidial length, slightly wider medially. Occipital furrow deep with weak forward flexure medially. L1 0.35 times glabellar length. S1 strongly convex, weakly impressed to indistinct adjacent to axial furrow, moderately impressed and directed diagonally (posteromedially) abaxially. S2 a very weak depression adjacent to axial furrow or indistinct, rarely extending adaxially, transverse. Axial furrows shallow to indistinct and directed obliquely opposite paraglabellar area and across occipital furrow, deep anteriorly. Paraglabellar area weakly defined. Preglabellar field flat (tr. sect.). Length (exsag.) of posterior border equal to occipital length adaxially, lengthening to 1.5 times occipital length abaxially. Posterior border furrow transverse, very wide, moderately impressed, terminating distally. Postocular fixigenal area long, length (exsag.) 0.21 times cranidial length. Palpebral lobe 0.14 times cranidial length, δ – δ 1.64 times glabellar width, palpebral furrow indistinct. Preocular fixigenal area of moderate width, 0.17 times δ – δ , narrowing markedly anteriorly, eye ridges not distinct. Anterior branches of facial suture meeting connective sutures opposite 0.9 cephalic length. Librigena with wide, moderately impressed border furrow anterior of eye, not defined opposite preglabellar field, librigenal field weakly convex, steeply inclined.



Dorsal section of connective sutures diverging at about 90°. Dorsal surface of rostral plate length (sag.) 0.5 times cranial length, very weakly concave (tr. sect.). Rostral suture moderately convex. Ventral surface of rostral plate kite-shaped, with length 0.9 times width, posterior width 0.1 maximum times width. Connective sutures angular, anterior section converging posteriorly at about 30°, posterior section converging posteriorly at about 70°. Librigenal doublure with wide, shallow vincular furrow, indistinct anteriorly. Hypostomal suture broadly concave.

Hypostome with length 0.75 times width, anterior wings large, width 0.35 times hypostomal width.

Thorax with thirteen segments. Axial furrows defined by shallow to moderately impressed, diagonally directed furrows on each segment, each meeting posterior margin at indentation that correspond to deep pits (axial articulating process) on internal mould. Pleural furrows wide and deep, pleural tips rounded.

Pygidium triangular, with sides weakly concave. Pygidial axis with sides straight and tapering at about 30°. Axis reaching 0.85 times pygidial length. Terminal piece parabolic in outline, length 0.08 times axial length, posterior margin moderately to weakly defined. Postaxial ridge not defined. Ring furrows short (sag.) and deep. Pleural furrows wide and deep adjacent to axial furrows, shallowing markedly abaxially, reaching wide and very shallow border furrow. Interpleural furrows very weakly defined. Border weakly defined. Pygidial doublure flat and weakly inclined posteriorly, laterally with angular profile (tr. section), distal surface horizontal, proximal surface increasingly inclined anteriorly. In posterior view anterior margin of pygidium moderately convex, posterior margin without distinct medial arch.

Remarks. Gill's (1949) original description is not detailed but documents most of the characters listed in the revised diagnosis. Gill described the glabellar furrows as absent, but the proximal portion of S1 is manifest as a short, moderately impressed diagonal furrow.

Trimerus (Edgillia) kinglakensis can be closely compared to the poorly known *T. (E.) vanuxemi* from the Helderbergian of North America. In addition to the shared cephalic and pygidial features listed above as defining *T. (Edgillia)*, the species share a forwardly convex rostral suture, a similar pygidial rib-ring offset (third–fourth? rib). The species differ in that *vanuxemi* exhibits longer glabellar proportions, shorter cephalic and pygidial proportions, a greater number of pleural ribs, a wider pygidial axis, and lacks a produced pygidial tip. In the depth of the pygidial axial furrows and ring and pleural furrows, *kinglakensis* shows closer resemblance to *T. (E?) major*, also from the Helderbergian of North America. However, *major* differs from *kinglakensis* in that the pleural furrows do not

shallow abaxially. Pygidial morphology of the Late Silurian *T. (E.) mongolicus* is closely comparable to that of *kinglakensis*. The Mongolian species exhibits similar proportions, 13 pygidial axial rings, deep ring furrows and shallow pygidial pleural furrows and an acuminate tip. *T. (E.) kinglakensis* differs in having deeper pygidial axial furrows, a shorter preglabellar field, and in the strong convexity of the rostral suture. Although the course of the rostral suture has been emphasised in the diagnoses of higher taxa (e.g. medial flexure in *Burmeisteria*, concavity in *Digonus*: see discussion above), variability in the forward curvature of the rostral suture amongst *Trimerus* is considered only of specific significance. Apart from *kinglakensis* and *vanuxemi*, few species of *Trimerus* exhibit strongly forwardly convex rostral sutures, the most notable exceptions being the type species *T. (T.) delphinocephalus* and *T. (T.) flexuosus*. Other features of these latter species are considered characteristic of *T. (Trimerus)* and *T. (Ramiotis)* respectively, and indicate that they are not closely related to *kinglakensis*.

Environmental notes. See discussion on taphonomy and biofacies. *Trimerus (Edgillia) kinglakensis* is considered to have inhabited mid- to outer-shelf environments.

Trimerus (Edgillia) jelli sp. nov.

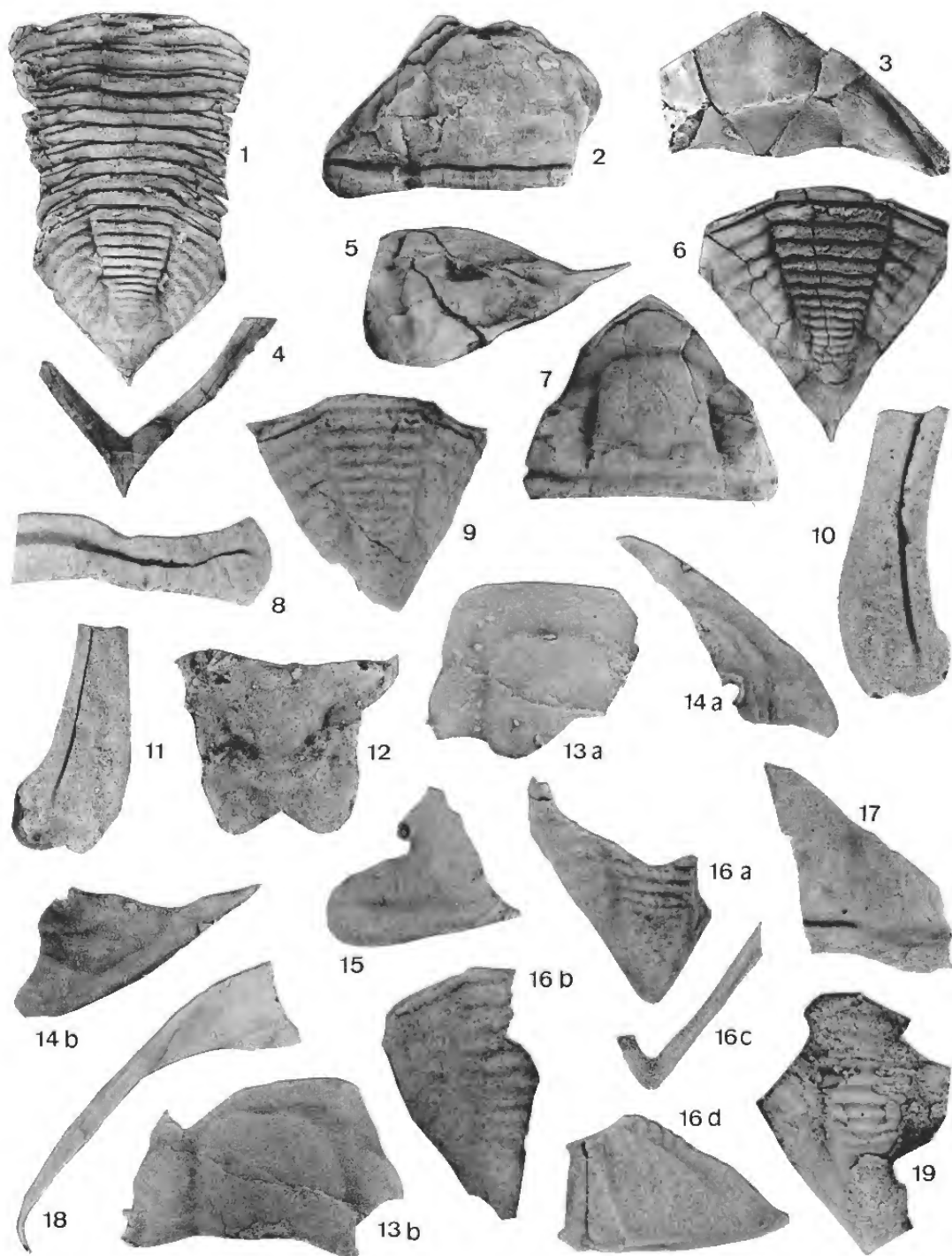
Figure 17.8–17.19

Homalonotidae gen. et sp. indet. 3—Holloway and Neil, 1982: 146, fig. 4M–R.

Type material. Holotype NMV P82873 (pygidium) from PL2288, Thomas locality F25, Parish of Redcastle, Heathcote, Victoria (Fig. 17.9). Paratypes NMV P78300 (ex GSV48930, figured Holloway and Neil, 1982: fig. 4R), NMV P304610 (cranidia), NMV P304612 (thoracic segment), NMV P78298 (pygidium, ex GSV48942, figured Holloway and Neil, 1982: figs 4M, 4N, 4Q) from PL2319, Thomas locality F55, Parish of Redcastle, Heathcote. Paratypes NMV P304638 (cranidium), NMV P304633–4 (librigenae), NMV P304635 (hypostome), NMV P304636, P304637 (thoracic segments), NMV P304639 (pygidium) from PL6652, Heathcote. Paratype NMV P78299 (librigena, figured Holloway and Neil, 1982: figs 4O, 4P) from PL2288. For localities see Fig. 8.

Registered material. 45 specimens: 6 cranidia, 3 librigenae, 1 hypostome, 25 thoracic segments, 8 pygidia. NMV P82925 (ex GSV48928), NMV P304610–P304625, NMV P304626 (ex GSV48933), GSV48944, GSV48938 from PL2319. NMV P82873, NMV P304628–P304632 from PL2288. NMV P304633–P304647 from PL6652. Unregistered specimen from PL2328, Heathcote.

Figure 16. *Trimerus (Edgillia) kinglakensis* (Gill, 1949). 1, NMV P305261, cranidium, dorsal view $\times 0.6$ (internal mould) from PL252. 2a, NMV P305257, cephalon and hypostome, dorsal view of cephalon $\times 0.75$ (latex cast) from PL252. 2b, same, dorsal view of hypostome $\times 1.6$. 2c, same, ventral view of cephalon (doublure) and hypostome $\times 1.4$. 3, NMV P305256, cephalothorax, dorsal view of cephalon $\times 0.85$ (latex cast) from PL252. 4, NMV P305262, cephalon, dorsal view $\times 0.85$ (latex cast) from PL252. 5, NMV P305265, cephalon, hypostome and displaced thoracopygon, dorsal view of hypostome $\times 1.55$ (latex cast) from PL252. 6a, NMV P305250, cephalon, dorsal view $\times 0.95$ (latex cast) from PL252. 6b, same, lateral view $\times 1.0$. 7a, NMV P305264, pygidium, posterodorsal view $\times 0.85$ (latex cast) from PL252. 7b, same, lateral view $\times 1.4$. 8, NMV P305248, cephalon, ventral view (doublure) $\times 1.0$ (latex cast) from PL252. 9, NMV P305252, cephalon, oblique view $\times 0.7$ (internal mould) from PL252. 10, NMV P305272, cephalon, dorsal view $\times 3.1$ (internal mould) from PL252. 11, NMV P305260, thoracopygon, dorsal view of pygidium $\times 0.7$ (latex cast) from PL252. 12, holotype NMV P14580, cephalon, dorsal view $\times 0.75$ (internal mould) from PL252. 13, NMV P305258, thoracopygon, dorsal view $\times 0.6$ (latex cast) from PL252. 14a, NMV P305263, pygidium, dorsal view $\times 1.1$ (latex cast) from PL252. 14b, same, $\times 1.0$ (internal mould). 15, NMV P305253, cephalon, ventral view (doublure) $\times 1.6$ (latex cast) from PL252. 16, NMV P305254, cephalon, dorsal view, enlargement of anterior margin $\times 2.9$ (latex cast) from PL252.



Stratigraphic distribution. Stoddart Member, Mt Ida Formation, 200 m to 500 m above the base of the unit, *Boucotia australis* Assemblage Zone, mid-late Lochkovian.

Derivation of name. For Peter Jell (Queensland Museum), for his contribution to Victorian palaeontology.

Diagnosis. Glabella with very weakly defined lobation, sides straight and converging at about 15°, anterior margin well defined, transverse, with broad medial depression. Axial furrows poorly defined posteriorly. Preglabellar field long, length 0.45 times anterior width of glabella (estimated 0.25 times cranidial length). Anterior branches of facial suture converging at 40°. Anterior margin of cranidium (including rostral suture) transverse. Palpebral lobe placed with midline opposite (estimated) 0.35 cranidial length. Hypostome with large, broad-based rounded lobes on the posterior margin. Thoracic pleurae with bilobed tips. Pygidium triangular, length equalling width, sides straight, converging at 60°. Axis with 10 rings, width 0.46 times pygidial width, length 0.8 (estimated) times pygidial length. Axial furrows very shallow. 6 pleural ribs. Pleural offset at third rib. Ring furrows moderately impressed, pleural furrows very shallow to indistinct, increasingly so posteriorly.

Discussion. Although most specimens assigned to this species are fragmentary, the morphology is distinctive enough to warrant description. The weakly convergent glabellar sides, the transverse and well-defined anterior margin and the simple glabellar morphology support assignment to *Edgillia*.

In cephalic features *Trimerus (Edgillia) jelli* differs from *T. (E.) kinglakensis* and *T. (E.) vanuxemi* in the transverse course of the rostral suture. Pygidial axial, ring and pleural furrows of *vanuxemi* are moderate to shallow in depth. In *kinglakensis*, the axial furrows and ring furrows are deep, with pleural furrows shallower, and markedly shallowing distally. The pygidium of *jelli* also exhibits pleural furrows shallower than the ring furrows, but is distinctive in that the pleural furrows are very shallow. The weakly defined segmentation is comparable to that of the Llandovery-lower Wenlock species of *T. (Ramiotis)*, although *jelli* differs from these in having a more elongate pygidial outline and in lacking the raised postaxial ridge typical of *T. (Ramiotis)*. In these respects the pygidia of *jelli* more closely resemble pygidia of species assigned in this work to *Burmeisteria*, in particular *B. clarkei* and *B. lineares*.

However, the strong segmentation shared by *clarkei* and *lineares* suggest that similarities in the pygidial outline and depth of pygidial axial ring and pleural furrows are not of high taxonomic significance. The distinctive (straight-sided, weakly furrowed) pygidial morphology shared by these three taxa and others such as *Dipleura garratti* suggests the morphology is homologous.

Hypostomes are known for few species of *Trimerus*. The hypostome of *T. (Edgillia) jelli* (Fig. 17.12) closely resembles that of *T. (E.) kinglakensis* (Fig. 16.2). These both differ from the hypostome of *T. (T.) delphinocephalus* (Whittington, 1993: fig. 1B) and *T. (Ramiotis) rickardsi* (Fig. 18.6) in having larger posterior border lobes and deeper middle furrows.

Environmental notes. *Trimerus (Edgillia) jelli* is considered to have inhabited high-energy, very shallow environments.

***Trimerus (Ramiotis)* subgen. nov.**

Type species. *Trimerus (Ramiotis) rickardsi* sp. nov., from the upper Llandovery (*crenulata* Biozone) Chintin Formation, central Victoria, Australia.

Other species included. *Platycoryphe dyaulax* Thomas, 1977, *Trimerus (Ramiotis) iani* sp. nov., *T. permutus* Tomczykowa, 1978 (nom. nov. for *T. lobatus* Tomczykowa, 1975 non Prouty, 1923), *T. (R.) otisi* sp. nov., *T. (R.) tomczykowae* sp. nov., *T. (R.) thomasi* sp. nov., *T. sp.* (in Edgecombe and Fortey, 2000), *T. sp.* (in Curtis and Lane, 1998), *T. sp.* A (in Wolfart, 1961),

Other species tentatively included. *Dipleura salteri* Morris, 1988 (nom. nov. for *Homalonotus (Koenigia) ludensis* Salter (1865) non *H. ludensis* Murchison, 1839).

Range. Silurian.

Derivation of name. For my son Otis Rami.

Diagnosis. Glabella trapezoid or weakly expanded across L1-L1 (tr.), low, with sides more or less straight and weakly to moderately convergent. S1-S3 weakly impressed. Preglabellar field of short to moderate length (~0.15–0.25 times cephalic length). Hypostomal middle furrow shallow. Pygidium short, length 0.5–1.0 times width. Postaxial ridge raised. Pygidium with moderately acute to obtusely convergent sides (>70°), tip without process or spine. Pygidial border furrow and ridge-like border present in late species.

Figure 17.1–17.7 *Trimerus (Edgillia) kinglakensis* (Gill, 1949). 1, NMV P305264, thoracopygon, dorsal view × 0.65 (latex cast) from PL252. 2, NMV P14584, inverted cephalon and displaced thoracopygon, dorsal view of cephalon × 0.9 (internal mould) from PL252. 3, NMV P305276, cephalon and displaced, incomplete thorax, ventral view of cephalon (doubleure) × 1.6 (latex cast) from PL252. 4, NMV P305269, incomplete thoracopygon, ventral view of pygidium (doubleure) × 0.85 (latex cast) from PL252. 5, NMV P305252, cephalon, lateral view × 0.6 (internal mould) from PL252. 6, NMV P305255, cephalon and displaced thorax, dorsal view of cephalon × 0.85 (latex cast) from PL252. 7, NMV P305258, thoracopygon, dorsal view of pygidium × 0.95 (latex cast) from PL252.

Figure 17.8–17.19 *Trimerus (Edgillia) jelli* sp. nov. 8, paratype NMV P304612, thoracic segment, dorsal view × 1.55 (internal mould) from PL2319. 9, holotype NMV P82873, pygidium, dorsal view × 1.4 (internal mould) from PL2288. 10, paratype NMV P304636, thoracic segment, lateral view × 2.0 (internal mould) from PL6652. 11, paratype NMV P304637, thoracic segment, lateral view × 1.9 (internal mould) from PL6652. 12, paratype NMV P304635, hypostome, ventral view × 2.0 (internal mould) from PL6652. 13a, paratype NMV P304610, cranidium, dorsal view × 1.3 (latex cast) from PL2319. 13b, same, × 1.35 (internal mould). 14a, paratype NMV P304634, librigena, dorsal view × 1.45 (latex cast) from PL6652. 14b, same, lateral view × 1.4. 15, paratype NMV P78300, cranidium, dorsal view × 1.1 (internal mould) from PL2319. 16a, paratype NMV P78298, pygidium, dorsal view × 1.25 (internal mould) from PL2319. 16b, same (latex cast). 16c, same, ventral view (doubleure) × 1.0 (internal mould). 16d, same, lateral view × 1.0. 17, paratype NMV P304638, cranidium, dorsal view × 1.25 (internal mould) from PL6652. 18, paratype NMV P304633, librigena, ventral view (doubleure) × 1.25 (latex cast) from PL6652. 19, paratype NMV P304639, pygidium, dorsal view × 5.5 (internal mould) from PL6652.

Discussion. Thomas (1977) noted that the rarity of Ashgill and Llandovery homalonotids emphasised the morphological gap between Ordovician and post-Ordovician genera. Reed (1918) suggested that links between Wenlock *Trimerus* and Ordovician homalonotid groups might be found in Llandovery strata. In this context Thomas interpreted his new Saudi Arabian Llandovery species *Platycoryphe dyaulax* as showing features of both *Platycoryphe/Brongniartella* and *Trimerus*. Thomas suggested that post-Ordovician homalonotines were derived from *Platycoryphe/Brongniartella* stock, rather than from *Eohomalonotus* as suggested by Szdzy (1957). In assigning *dyaulax* to *Platycoryphe*, Thomas emphasised its wider and rounded pygidial outline, contrasting with the longer and posteriorly pointed outlines of 'typical' *Trimerus*, i.e. *T. (Trimerus)*. Pygidia of *dyaulax* also exhibit shallow ring furrows and very shallow to effaced axial and pleural furrows, whereas pygidia of *T. (Trimerus)* exhibit pleural and ring furrows of moderate depth, and of equal depth.

New species from the Llandovery and lower Wenlock of south-eastern Australia show strong resemblances to *Platycoryphe dyaulax* and define a tight species group. Similarities in cephalic morphology between *dyaulax* and *Trimerus* noted by Thomas are emphasised by the new Llandovery-Wenlock taxa, and all share weakly tapering, straight-sided, trapezoid glabellar outlines. The new south-eastern Australia taxa exhibit pygidial proportions and segmentation intermediate between *dyaulax* and *T. (Trimerus)* and support Thomas's suggestion of close affinities between *dyaulax* and *Trimerus*. These similarities, and the weak definition of thoracic trilobation, the width of the thoracic axis and the lower degree pygidial segmentation are emphasised here to justify assignment of *dyaulax* to *Trimerus* rather than to *Platycoryphe* or *Brongniartella*. *T. (Ramiotis)* is erected to embrace this group of species, which includes late Llandovery *T. (R.) rickardsi* from Victoria and *T. (R.) iani* from Tasmania, and the early Wenlock *T. (R.) tomczykowae* from Victoria.

In pygidial outline and segmentation there is a morphological gradient through time from *Trimerus (Ramiotis) dyaulax* (mid Llandovery) to *T. (R.) rickardsi* and *T. (R.) iani* (late Llandovery) with moderately impressed ring and axial furrows and shallow pleural furrows, to *T. (R.) tomczykowae* (early Wenlock) with pygidial furrows of subequal and moderate depth, and to *T. (Trimerus)* (Wenlock-early Ludlow). Although *T. (Trimerus)* appears to be derived from this group, there are a number of new or poorly known Ludlow-Prídolí *Trimerus* that share the distinctive cranial morphology of the Llandovery-Wenlock *T. (Ramiotis)*. In exhibiting elongate glabellar proportions, weakly tapered, straight-sided trapezoid glabellar outlines, low glabellar profiles and prelabellar fields of moderate length, these species are compatible with assignment to *T. (Ramiotis)* rather than to *T. (Trimerus)*. These species include *T. (R.) otisi* and *T. (R.) thomasi* from Victoria, *T. (R.) permutus* from Poland, and *T. (R.) sp. (in Wolfart, 1961)* from Bolivia. Compared with the Llandovery-Wenlock *T. (Ramiotis)*, these Ludlow-Prídolí species encompass a wider range of pygidial morphologies, particularly in length:width proportions and depth of pygidial furrows.

Trimerus (Ramiotis) is easily distinguished from *T. (Trimerus)* in that it lacks most of the characteristic cephalic and pygidial features of the latter. Of the suite of features listed as diagnostic for *T. (Trimerus)*, only *T. (R.) permutus* exhibits strongly expressed glabellar lobation. Several species exhibit sagittal glabellar ridges (albeit weak), several species exhibit distinct medial indentations of the anterior glabellar margin, and some specimens of *T. (R.) otisi* show a tendency towards outlines expanded across L1-L1 (tr.) and strongly tapered glabellar outlines. However, there are no species of *T. (Ramiotis)* that exhibit a more than a few of the characters of *T. (Trimerus)*, justifying the grouping of the latter. However, with the exception of the deep pygidial border furrow and raised border, the characters distinguishing *T. (Ramiotis)* from *T. (Trimerus)* can be considered as primitive, and hence only subgeneric status is justifiable.

Dipleura salteri Morris, 1988 from the upper Ludlow (Ludfordian) of England is a poorly known species represented by a single cranium (see Salter, 1865: p. 121, pl. 12 fig. 1). Following Salter's (1865) suggestion, Tomczykowa (1975) and Morris (1988) assigned the species to *Dipleura*, but the forward eye position, the long prelabellar field and the quadrate course of the preocular facial sutures preclude assignment to that genus and are in accord with assignment to *Trimerus*. Subgeneric assignment of *salteri* is difficult as the species exhibits a very strongly tapered glabellar outline comparable to that of *T. (Trimerus)*, but lacks the other diagnostic glabellar features of the subgenus such as the outline strongly expanded across L1-L1 (tr.) and the distinct lobation. However, the strong tapering of the glabella may be partly attributable to sagittally oriented tectonic compression evident in the apparent concavity (sag.) of the prelabellar field. In all other respects the specimen is compatible with assignment to *T. (Ramiotis)*, to which it is tentatively assigned.

Trimerus (Ramiotis) dyaulax is from the Aeronian (mid-Llandovery) *convolutus* Biozone. A possibly earlier origin for *Trimerus* is suggested by a poorly known species from the lower Llandovery of Paraguay. Wolfart (1961) assigned the several cranidia representing this species to *Trimerus*. In having elongate glabellar proportions, weakly tapered, straight-sided trapezoid glabellar outlines, weak glabellar lobation and a prelabellar field of moderate length, these can be assigned to *T. (Ramiotis)*. The only other Llandovery *T. (Ramiotis)* is represented by fragmentary pygidia from the Aeronian of Wales, documented as *T. sp.* by Curtis and Lane (1998). Although closer in age to *dyaulax*, the Welsh species differs markedly from it in having moderately impressed pleural, ring and axial furrows, in this respect closely resembling *T. (R.) rickardsi*.

Trimerus (Ramiotis) rickardsi sp. nov.

Figure 18

Type material. Holotype NMV P305556 (cephalon) from PL6361, Springfield, Victoria (Fig. 18.1). Paratypes NMV P305553, P305554, NMV P305557, NMV P305563 (cephala), NMV P305559–P305562, NMV P305564 (cranidia), NMV P305582 (thoracic segment), NMV P305572–P305574 (pygidia) from PL6361. Paratype NMV P138204 (pygidium) from PL667, Springfield. Paratype NMV P138207 (pygidium) from PL599, Springfield. Paratypes NMV P147779

(hypostome), NMV P147772 (pygidium) from PL256, Wallan, Victoria. For localities see Fig. 11.

Registered material. 66 specimens. 5 cephalae, 15 cranidia, 6 librigenae, 1 rostral plate, 3 hypostomes, 12 thoracic segments, 24 pygidia. NMV P305553–P305593 from PL6361. NMV P305626–P305628 from PL6390, Springfield. NMV P138213, NMV P147771, P147772, NMV P147774–P147777, NMV P147779–P147780, NMV P1477787 from PL256. NMV P139442–P139446, NMV P305595 from “Lancefield”, Victoria. NMV P138205–P138207, NMV P138270 from PL599. NMV P138204, NMV P305594 from PL667. NMV P138267, NMV P147778 from PL1964, GSV locality B25, Springfield. Lithological similarities suggests that the specimens labelled as coming from “Lancefield” almost certainly come from the Parish of Goldie, and possibly in the vicinity of allotments B19 and B23 (see Thomas, 1960: 1:31, 680 Lancefield Geological Sheet).

Stratigraphic horizon. Chintin Formation, upper Llandovery. Rickards and Sandford (1998) suggested equivalence to the upper *crenulata* Biozone, based on the presence of *Aceraspis* sp. within the unit, and on the occurrence of *crenulata* Biozone graptolites in the uppermost beds of the underlying Springfield Sandstone.

Derivation of name. For R. B. Rickards (University of Cambridge), for his contribution to Victorian palaeontology.

Diagnosis. Cephalon rounded pentagonal, width about 1.6 times length, sides converging at 60° posteriorly, at 125° anteriorly. Glabella trapezoid, length 1.2 times width, sides subparallel opposite paraglabellar areas, converging anteriorly at about 22°. S1–S3 moderately impressed adjacent to the axial furrow, shallow adaxially. Preglabellar field long, 0.23 times cephalic length. Palpebral lobes placed opposite 0.42 cranial length/0.52 glabellar length. Anterior branches of facial suture straight, converging at about 45°, anterior-most section curving gently to the diagonal, continuous in curvature with broadly rounded rostral suture. Dorsal section of rostral plate crescentic, length 0.1 times cephalic length. Ventral section of rostral plate with length 0.92 times width, connective sutures converging posteriorly at 50°. Posterior border of hypostome with short lobes of length 0.1 times hypostomal length. Pygidium wide, length 0.78 times width, with sides weakly convex, converging posteriorly at about 100°. Pygidial axis 0.42 times pygidial width, with 10 axial rings. Axial furrows straight, tapering at about 30°, shallow anteriorly, moderately impressed posteriorly. Ring furrows deep to moderately impressed, pleural furrows shallow. 7–8 ribs, rib-ring medially offset at fourth rib.

Description. Exoskeleton small, maximum length 12 cm (estimated from NMV P138204), occipital and pygidial convexity (tr.) moderate. Dorsal exoskeleton and doublure finely granulose.

Cranidium with length (sag.) 0.9 times cephalic length. Glabella trapezoid, length about 0.77 times cranial length, width about 0.43 times cranial width, anterior margin moderately well defined, broadly rounded, medial indentation variably expressed (indistinct to strong, e.g. NMV P305559). Glabellar lobation well defined. Occipital ring 0.09 times glabellar length, slightly wider medially. Occipital furrow deeply impressed with broad forward flexure medially. L1 ~0.3 times glabellar length, L2 and L3 ~0.1 times glabellar length and frontal lobe ~0.25 times glabellar length. S1 weakly convex forwards and directed posteromedially at about 25° from the transverse. S2 transverse. S3 directed antero-medially at about 10° from the transverse. Axial furrows moderately impressed opposite genae, shallow

and directed diagonally opposite occipital ring. Paraglabellar area very weakly defined. Length (exsag.) of posterior border equal to occipital length adaxially, lengthening (exsag.) markedly abaxially to about twice occipital length. Posterior border furrow transverse, very wide, moderately impressed, terminating distally. Postocular fixigenal area with length (exsag.) 0.22 times cranial length. Palpebral lobe short, 0.1 times cranial length, placed with δ - δ about 1.77 times pre-occipital glabellar width/0.74 times cephalic width. Palpebral furrow wide and shallow. Preocular fixigenal area narrow (tr.), 0.17 times δ - δ , uniform in width anteriorly. Preglabellar field flat (tr. sect.). Anterior branches of facial suture straight from eye to a point opposite midlength (sag.) of preglabellar field, anterior section curved. Librigenal border furrow wide and shallow opposite genal field, not defined opposite preglabellar field, border furrow indistinct on fixigenae. Lateral border narrow and convex, narrowing posteriorly, indistinct opposite preglabellar field and on fixigenae. Dorsal surface of rostral plate with length 0.13 times width, anterior margin rounded. Dorsal section of connective sutures diverging forwards at about 30°. Ventral surface of rostral plate flat (tr, sag. sect.), kite-shaped, sides very weakly sinusoidal. Librigenal doublure without distinct vincular furrow. Hypostomal suture transverse.

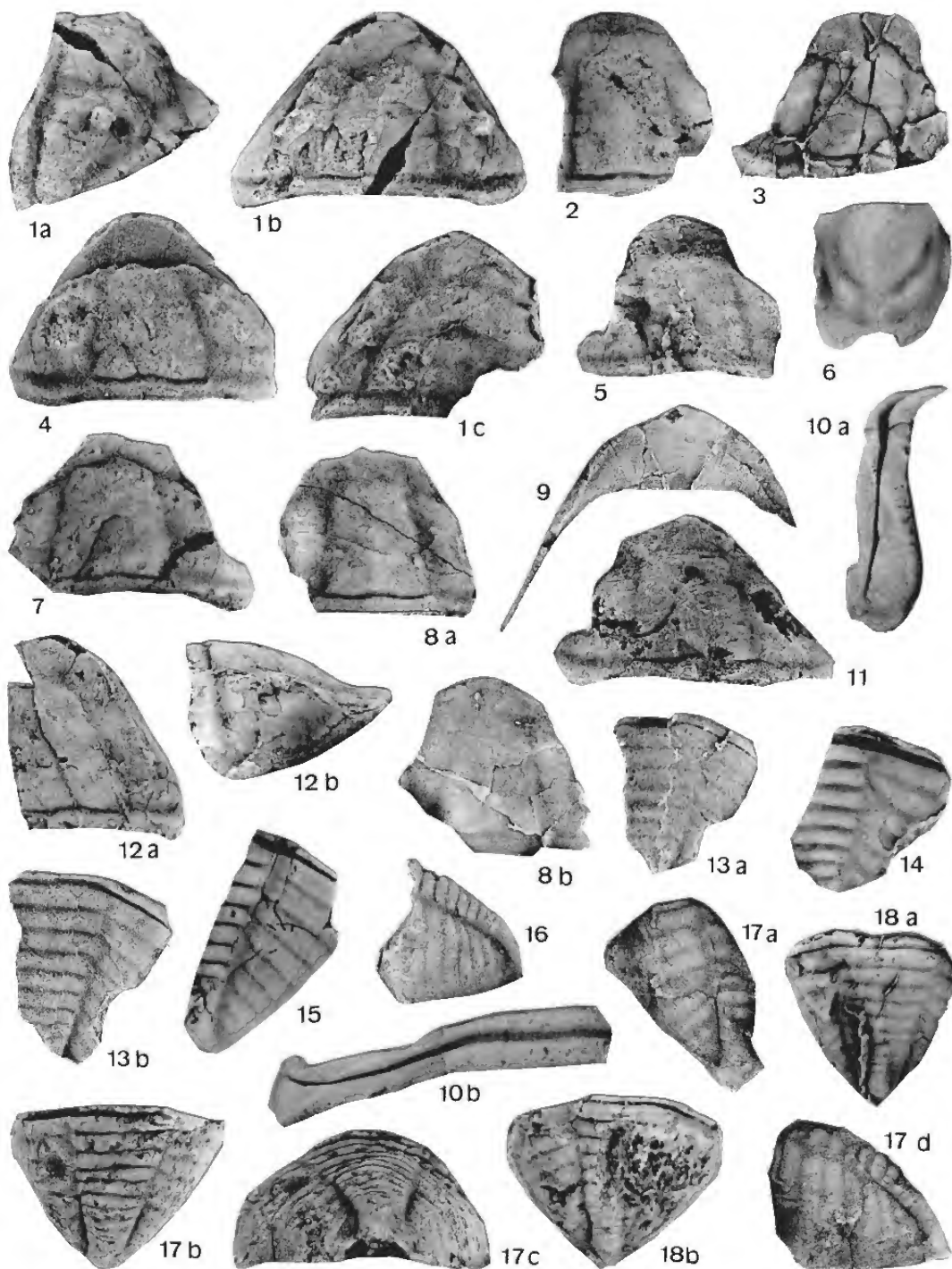
Hypostome with moderately impressed middle furrow.

Thoracic segments with wide (sag.), deep articulating furrows, deep and narrow (exsag.) pleural furrows. Axis very weakly defined by very shallow, wide, diagonally directed furrow. Pleural tips weakly bilobed with larger lobe opposite posterior band and smaller lobe opposite anterior band.

Pygidium triangular. Pygidial axis extending to about 0.9 pygidial length, with semicircular terminal piece, length 0.1 times axial length, continuous posteriorly with raised postaxial ridge. Ring furrows deep to moderately impressed, pleural furrows shallow. Furrows markedly shallower on external casts. Pleural furrows not reaching margin. Border furrow and border poorly defined. In posterior view posterior margin of pygidium horizontal. In lateral view dorsal profile of axis moderately convex, postaxial ridge steeply inclined.

Discussion. *Trimerus (Ramiotis) rickardsi* is the most completely known homalonotid from the Llandovery. The species is of primary significance in the understanding of relationships between poorly known Llandovery homalonotids and better-known Wenlock and Ludlow taxa.

In pygidial morphology *Trimerus (Ramiotis) rickardsi* is typical of other Llandovery–Wenlock species, particularly in having short pygidial proportions and much shallower ring furrows relative to the pleural furrows. In the latter feature *rickardsi* most closely resembles the very poorly known Welsh *T. (R.)* sp. (see Curtis and Lane, 1998), but can be distinguished by its higher segmentation (7 rings, 6 ribs in *T. (R.)* sp., cf. 10 rings, 8 ribs in *rickardsi*). *T. (R.) dyaulax* differs from *rickardsi* in having even shorter proportions, a rounded pygidial tip, a low postaxial ridge, even shallower axial, ring and pleural furrows and lower segmentation (6 rings, 5 ribs) than counted for *rickardsi*. Pygidial morphology of *T. (R.) iani* from the upper Llandovery of Tasmania is poorly known. The single pygidium known exhibits segmentation comparable (9 rings, 6 ribs) to that of *rickardsi*, but differs in having shorter proportions and a rounded tip. The relative depth of the ring furrows compared to the pleural furrows distinguishes *rickardsi* from the Wenlock *T. (R.) tomczykowae* from Victoria, and from other Ludlow species of *T. (Ramiotis)*. *T. (R.) tomczykowae* further differs in having a more rounded tip. Of the Upper Silurian



species, *T. (R.) thomasi* from Victoria differs markedly in having elongate proportions (L:W~1.0), whilst pygidia of *T. (R.) otisi* from Victoria differ markedly in the depth of the pygidial pleural and ring furrows. Despite the pygidial differences, in the more elongate glabellar outline (L/W~1.2) the longer preglabellar field (0.25 cranial length), and the expression of glabellar lobation, *rickardsi* shows closest resemblance to *otisi*. *T. (R.) rickardsi* differs from most other *T. (Ramiotis)* in having a forwardly convex rostral suture, comparable to that of the Llandovery Bolivian *T. (R.)* sp.

In having a relatively longer preglabellar field, lateral glabellar furrows of moderate length, a weak sagittal glabellar ridge and, in some specimens, a distinct medial indentation of the anterior glabellar margin, and higher pygidial segmentation *Trimerus (Ramiotis) rickardsi* shows closer affinities to *T. (Trimerus)* than other Llandovery *T. (Ramiotis)*. However, in the absence of so many of the other derived features distinguishing *T. (Trimerus)*, it would be over stated to regard *rickardsi* as a transitional species between the subgenera.

Environmental notes. Articulated specimens are only known from the type locality, and represented only by cephalons. The proportion of articulated and broken specimens is 13% respectively, indicative of a taphofacies TII. Further east at PL256, Wallan, breakage of *T. (R.) rickardsi* and other trilobites is extremely high and indicates significant reworking. Associated tempestite lithologies comprising thick coquina bioclastic lags and abundant mud rip-up clasts indicate deposition between normal wave base and storm wave base. The trilobite fauna may have been transport, possibly in a tempestite-generated mass-flow, although the profound compositional differences between the Springfield, Wallan and Lancefield faunas do not support this and suggest distinct, depth-related assemblages. *Trimerus (Ramiotis) rickardsi* is considered to inhabit inner shelf environments.

Trimerus (Ramiotis) iani sp. nov.

Figures 19.1–19.4, 19.6

Trimerus sp.—Holloway and Sandford, 1993: 93, figs 4C–D, 4F–G, 4I–J, 4N–P, non fig. 4L.

Type material. Holotype NMV P137221 (cephalon lacking rostral plate, figured Holloway and Sandford, 1993: 4F–G, 4J, Fig. 19.1 herein) from PL359, Tiger Range, northwest of Maydena, Tasmania. Paratypes NMV P137222 (cranidium, figured Holloway and

Sandford: 4I), NMV P137227 (pygidium, figured Holloway and Sandford: 4N–P), NMV P137224 (cephalon, figured Holloway and Sandford: 4C), NMV P137223 (cephalon and two displaced thoracic segments) from PL359. For locality see Holloway and Sandford: fig. 1

Previously figured material. NMV P137225 (librigena, figured Holloway and Sandford, 1993: 4D) from PL359.

Other material. NMV P137226 (cephalon) from PL359.

Stratigraphic distribution. As for *Brongniartella* sp.

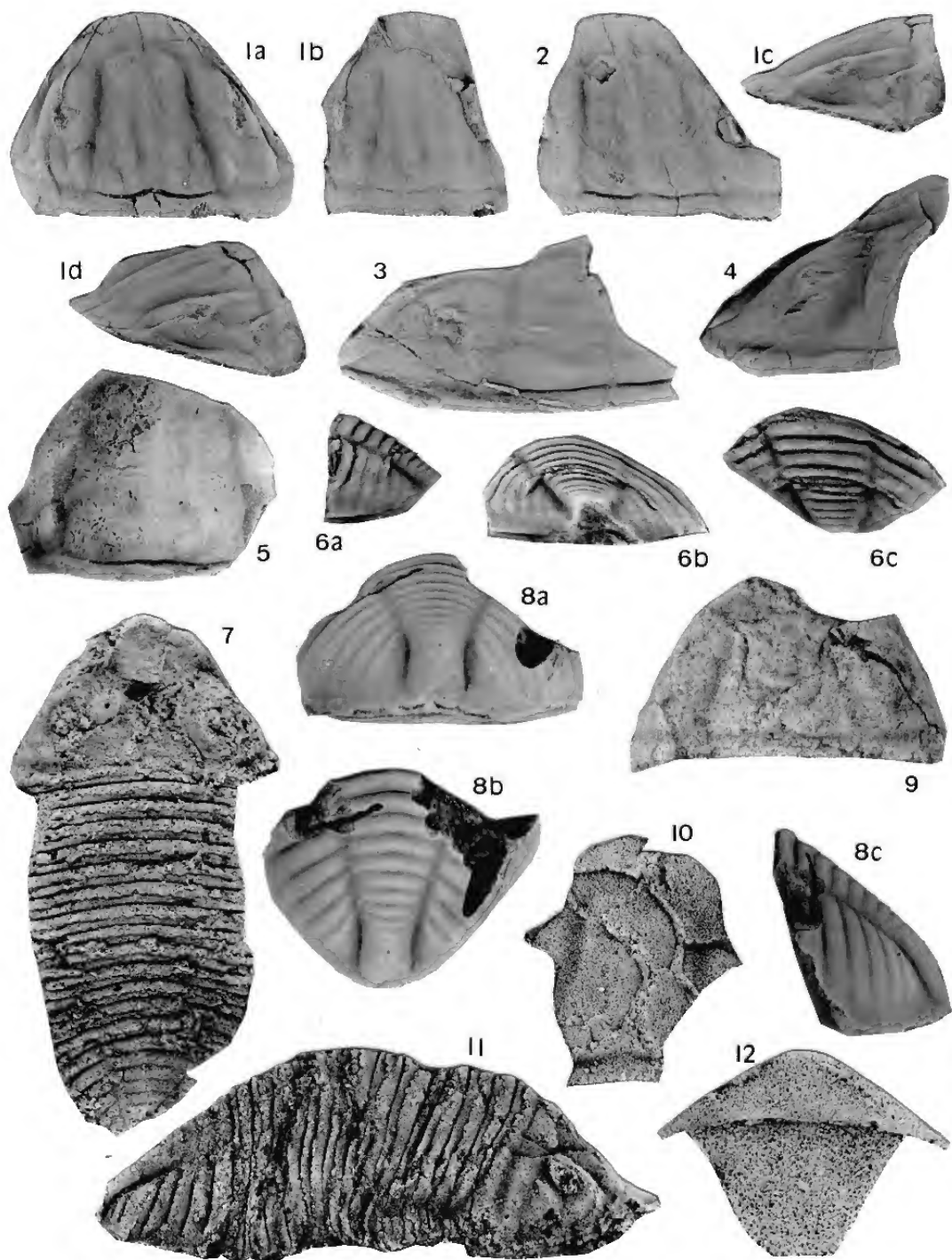
Derivation of name. For my brother Ian.

Diagnosis. Cephalon rounded triangular, length ~0.7 times width, sides (opposite midlength) converging at ~60°. Glabella trapezoid in outline, length 1.2 times width, sides very weakly concave and tapering at 20° anteriorly, anterior glabellar margin transverse, without distinct medial indentation. S1–S3 and sagittal glabellar ridge very weakly defined. Preglabellar field of moderate length (0.2 times cranial length), rostral suture transverse, dorsal section of rostral plate short, 0.05 times cephalic length. Eye placed opposite ~0.5 cranial length (~0.6 glabellar length). Anterior branches of facial sutures converging at 60°, curving abruptly adjacent to connective sutures. Ventral surface of rostral plate elongate pentagonal in outline, with connective sutures converging posteriorly at 45°. Pygidium short. Axis 0.45 times pygidial width, raised posteriorly, 10 rings, ring furrows moderately impressed. 6 ribs, pleural furrows shallow. Axial furrows moderately impressed.

Discussion. *Trimerus (Ramiotis) iani* is abundant at the type locality. Holloway and Sandford (1993) were uncertain whether the two dissimilar homalonotid pygidia from PL359 represented different species, or whether the differences were attributable to size differences or deformation. In reviewing this conclusion, I cannot attribute the contrast between the narrow, concave-sided and strongly raised axis of the smaller specimen (see Holloway and Sandford, 1993: fig. 4L) and the wide, convex-sided and low axis of the larger specimen entirely to deformation (see Fig. 19.6). The more elongate (length=width) and parabolic outline and the indication of a distinct border suggest that the smaller pygidium represents a separate species, referable to *Brongniartella* (see above).

The diagnosis includes a number of features not listed in the brief description of the species by Holloway and Sandford (1993). Of the two cephalons not figured by Holloway and

Figure 18. *Trimerus (Ramiotis) rickardsi* sp. nov. 1a, holotype NMV P305556, cephalon, oblique view $\times 1.7$ (internal mould) from PL6361. 1b, same, dorsal view. 1c, same (latex cast). 2, paratype NMV P305560, cranidium, dorsal view $\times 2.4$ (latex cast) from PL6361. 3, paratype NMV P305561, cranidium, dorsal view $\times 1.4$ (internal mould) from PL6361. 4, paratype NMV P305557, cephalon, dorsal view $\times 2.1$ (internal mould) from PL6361. 5, paratype NMV P305564, cranidium, dorsal view $\times 2.1$ (latex cast) from PL6361. 6, paratype NMV P147779, hypostome, ventral view $\times 2.7$ (latex cast) from PL256. 7, paratype NMV P305562, cranidium, dorsal view $\times 1.6$ (internal mould) from PL6361. 8a, paratype NMV P305559, cranidium, dorsal view $\times 1.5$ (internal mould) from PL6361. 8b, same, $\times 1.6$ (latex cast). 9, paratype NMV P305554, cephalon, ventral view (double) $\times 1.75$ (internal mould) from PL6361. 10a, paratype NMV P305582, thoracic segment, lateral view $\times 2.5$ (internal mould) from PL6361. 10b, same, dorsal view $\times 2.2$. 11, paratype NMV P305563, cephalon, dorsal view $\times 2.4$ (internal mould) from PL6361. 12a, paratype NMV P305553, cephalon, dorsal view $\times 1.5$ (internal mould) from PL6361. 12b, same, lateral view $\times 2.0$. 13a, paratype NMV P305573, pygidium, dorsal view $\times 1.9$ (latex cast) from PL6361. 13b, same, $\times 2.2$ (internal mould). 14, paratype NMV P147772, pygidium, dorsal view $\times 2.0$ (latex cast) from PL256. 15, paratype NMV P138204, pygidium, dorsal view $\times 1.4$ (internal mould) from PL667. 16, paratype NMV P305574, pygidium, lateral view $\times 2.5$ (latex cast) from PL6361. 17a, paratype NMV P138207, pygidium, dorsal view $\times 1.75$ (latex cast) from PL599. 17b, same, $\times 1.5$ (internal mould). 17c, same, posterior view $\times 1.75$. 17d, same, lateral view (latex cast). 18a, paratype NMV P305572, pygidium, dorsal view $\times 1.6$ (latex cast) from PL6361. 18b, same (internal mould).



Sandford, one specimen shows the anterior margin of the cephalon, with the impression of the rostral suture evident on the surface of the doublure (Fig. 19.4). The other specimen shows the posterior portion of the ventral surface of the rostral plate. The pygidial pleural furrows are shallow, although the greater depth of the first furrow appears to be partly exaggerated by longitudinal shearing.

Holloway and Sandford (1993) distinguished *Trimerus* (*Ramiotis*) *iani* from previously documented homalonotids from the Ludlow-Pragian strata of south-eastern Australia. Of the species discussed by Holloway and Sandford, only specimens described by Talent (1964) as "*Dipleura* sp." can be referred to *T. (Ramiotis)*.

In cephalic features *Trimerus* (*Ramiotis*) *iani* is similar to *T. (R.) otisi* from the Ludlow of Victoria. These species share a glabella with elongate proportions (L:W~1.2) and moderately tapering (~25°) and weakly concave sides, a preglabellar field of similar length (0.2 cranial length), similar cephalic proportions (L:W ~0.7), a transverse rostral suture, very short pygidial proportions and comparable pygidial segmentation. *T. (R.) otisi* differs in having well defined glabellar lobation and a distinctive tricuspid anterior cephalic margin. In cephalic features *T. (R.) permutus* from the Ludlow of Poland is also closely comparable, although it differs in having strongly expressed glabellar lobation. In pygidial features *iani* demonstrates its closer affinities to other Lower Silurian *T. (Ramiotis)*, particularly in the weak expression of the pleural furrows, the deeper ring furrows, and the rounded tip. In pygidial morphology *iani* is closest to *T. (R.) dyaulax*, that differs in having weaker segmentation. *T. (R.) iani* is closest in age to the type species *T. (R.) rickardsi*, but differs in having a shorter preglabellar field, weaker glabellar lobation, a transverse rostral suture, and a rounded pygidial tip.

Trimerus (Ramiotis) otisi sp. nov.

Figure 20

Homalonotus vomer.—Chapman, 1912: 298, pl. 63 fig. 1, non pl. 62 figs 2, 3, pl. 63 fig. 2.

Trimerus vomer.—Gill, 1949: 65, text-fig. 1B, non text-fig. 1C.

Trimerus cf. *tilydalisensis*.—Williams, 1964: 285, table 1.

Trimerus sp.—Garratt, 1968: 164, chart 1.

Trimerus cf. *vomer*.—Garratt, 1968: 164, chart 1.

Type material. Holotype NMV P304741 (cephalon and displaced thoracopygon) from PL1898, Eden Park, Victoria (Fig. 20.5). Paratypes

NMV P304727 (cephalon and displaced thoracopygon), NMV P304722–P304724 (cephala), NMV P304726 (cranidium), NMV P304718–P304720 (pygidia) from PL6633, Eden Park. Paratypes NMV P304739, NMV P304797 (incomplete cephalothoraxes), NMV P304738 (thoracopygon), NMV P304742 (pygidium) from PL1898. Paratypes NMV P304730, NMV P304733, P304734 (cephala), NMV P304729 (pygidium) from PL6632, Eden Park. Paratype NMV P304737 (pygidium) from PL300, Clonbinane, Victoria. For localities see Fig. 11.

Registered material. 141 specimens: 4 dorsal exoskeletons, 3 dorsal exoskeletons with displaced cephalo, 3 articulated cephalothoraxes, 2 thoraxes with displaced cephalo, 15 cephalo, 22 cranidia, 3 librigenae, 1 hypostome, 8 thoracic segments, 4 articulated thoraxes, 10 articulated thoracopygons, 66 pygidia. *Eden Park*: NMV P304766–P304770 from PL6627, Jutson locality VIII. NMV P304743, NMV P304775–P304778 probably from PL6627. NMV P304771–P304773 from PL6628. NMV P304832–P304836 from PL6629, Williams locality F130. NMV P304745, NMV P304837–P304840 from PL6630. NMV P304738–P304742, NMV P304779–P304799 from PL1898. NMV P304832–P304838 from PL6631. NMV P304728–P304736, NMV P304807–P304822 from PL6632. NMV P304718–P304727, NMV P304747–P304765 from PL6633. NMV P304800–P304806 from PL6635. NMV P304744 from "Eden Park". Unregistered specimens from PL6634 and PL6616, Williams locality X12. *Upper Plenty–Clonbinane area, Victoria*: NMV P304774 from PL6636, Jutson locality III=Williams locality F12, Upper Plenty. NMV P304746, NMV P304830, P304831 from PL6638, Kenley locality 32g, Upper Plenty. NMV P304844–P304846 from PL6639, Upper Plenty. NMV P304841–P304843 from PL6642, Williams locality G23, Wandong. NMV P304737, NMV P304823–P304826 from PL300. NMV P304827–P304829 from PL1782, Clonbinane. In addition, homalonotids recorded by Garratt (1968) from PL6618, Jutson locality IX=Williams locality F90, Eden Park and by Williams (1964) from Williams locality F41, Clonbinane undoubtedly refer to *Trimerus* (*Ramiotis*) *otisi*, although specimens from these localities are not represented in the MOV collections. *Humevale*: NMV P304851 from PL6646, Williams locality W17. Unregistered specimen from PL6648. For localities see Fig. 11.

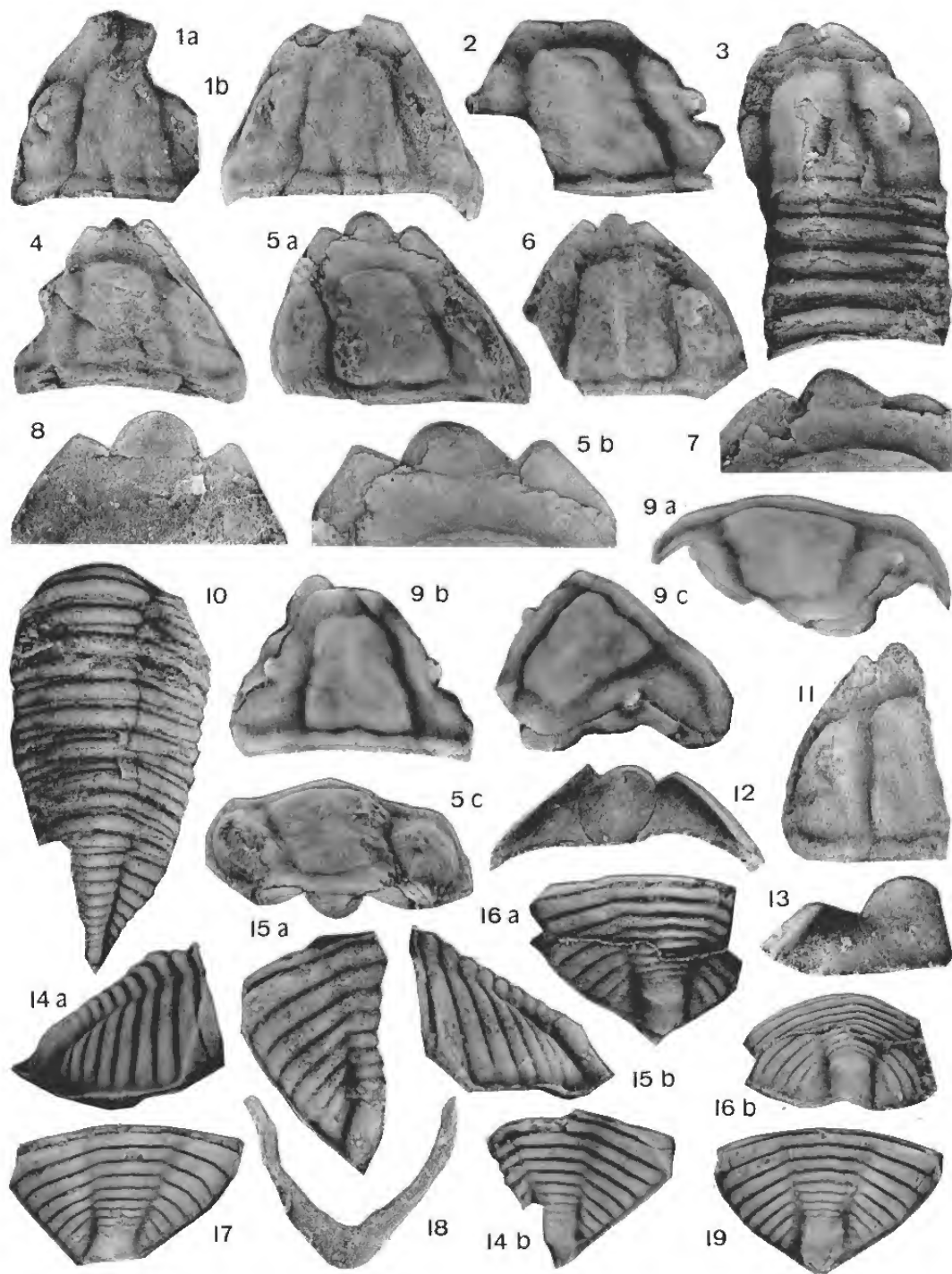
Stratigraphic distribution. Eden Park Formation, from 350 m above the base to the top of the unit, *Notoparmella plentiensis* Assemblage Zone, late Ludlow.

Diagnosis. Cephalon with length 0.7 times width, anterior margin tricuspid. Glabella trapezoid, length about 1.17 times width, sides converging at about 25°, anterior margin strongly defined, transverse. Glabellar lobation moderately well defined. Palpebral lobe placed opposite 0.6 glabellar length (0.5 cranial length). Moderately impressed sutural and

Figure 19.1–19.4, 19.6. *Trimerus (Ramiotis) iani* sp. nov. 1a, holotype NMV P137221, cephalon, dorsal view (internal mould) from PL359. 1b, same, oblique view. 1c, same, lateral view. 1d, same, dorsal view (latex cast). 2, paratype NMV P137224, cephalon, dorsal view (internal mould) from PL359. 3, paratype NMV P137222, cranidium, dorsal view (internal mould) from PL359. 4, paratype NMV P137223, cephalon, dorsal view (internal mould) from PL359. 6a, paratype NMV P137227, pygidium (internal mould) lateral view, from PL359. 6b, same, posterior view. 6c, same, dorsal view.

Figure 19.5, 19.8, 19.10, 19.12. *Trimerus (Ramiotis) tomczykowa* sp. nov. 5, paratype NMV P305191, cranidium, dorsal view × 1.1 (internal mould) from PL2263. 8, holotype NMV P138203, pygidium (internal mould) × 1.5, from the "Illaeus band", Costerfield South. 8a, posterior view. 8b, dorsal view. 8c, lateral view. 10, NMV P138291, cephalon (fragment), dorsal view (latex cast) from PL1460. 11, paratype NMV P138293, rostral plate, dorsal view × 6.0 (latex cast) from PL1460.

Figure 19.7, 19.9, 19.11. *Trimerus (Trimerus) harrisoni* (McCoy, 1876). 7, holotype NMV P7503, complete exoskeleton, dorsal view × 1.8 (internal mould) from PL1620. 9, NMV P136645, complete exoskeleton, dorsal view of cephalon with impression of hypostome × 2.1 (internal mould) from PL1620. 11, NMV P2500, complete exoskeleton, lateral view × 2.6 (internal mould) from PL1620.



sub-ocular furrows, weak eye ridges. Preglabellar field 0.2 times cranial length. Anterior branch of facial suture straight poster-iorly, converging at about 55°, then anteriorly curving strongly to the transverse, rostral suture transverse. Dorsal surface of rostral plate semicircular, without connective sutures, equal in length to preglabellar field. Ventral surface of rostral plate with length equalling width, connective sutures moderately convex and converging posteriorly at about 90°. Pygidium triangular, short, length 0.6 times width, with sides weakly convex and converging posteriorly at about 110° to an obtusely pointed tip. Pygidial axis narrow, width (measured across second ring) 0.3 times pygidial width, 10 axial rings, ring furrows deep. 7–8 pleural ribs, pleural furrows as deep as ring furrows and uniform in depth to lateral border furrow, rib-ring medially offset at fifth rib. Axial furrows moderately impressed posteriorly, poorly defined anteriorly, postaxial ridge posteriorly raised. Lateral border furrow well defined, border a raised ridge.

Discussion. The distinctive tricuspid cephalic margin immediately distinguishes *Trimerus (Ramiotis) otisi* from all other members of the genus. The pygidium of *otisi* is also distinguishes the species from many congeners, with deep pleural and ring furrows and the anteriorly indistinct axial furrow shared only with the Bolivian *T. (R.)* sp. A. The Bolivian species also displays a well defined border furrow and border comparable to that of *otisi* and *T. (R.) thomasi*, but the species differs in having longer pygidial proportions (L:W~0.9) and a wider pygidial axis (width 0.5 pygidial width). The very short pygidial proportions of *otisi* are closest to those of *T. (R.) iani*, that also shares comparable cephalic features including moderate length of the preglabellar field, longer glabellar proportions, a glabellar outline weakly expanded across L1-L1 (tr.), and a forward eye position (opposite 0.5 cranial length). In addition to the tricuspid margin, *otisi* differs from *iani* in having distinct subocular furrows and eye ridges.

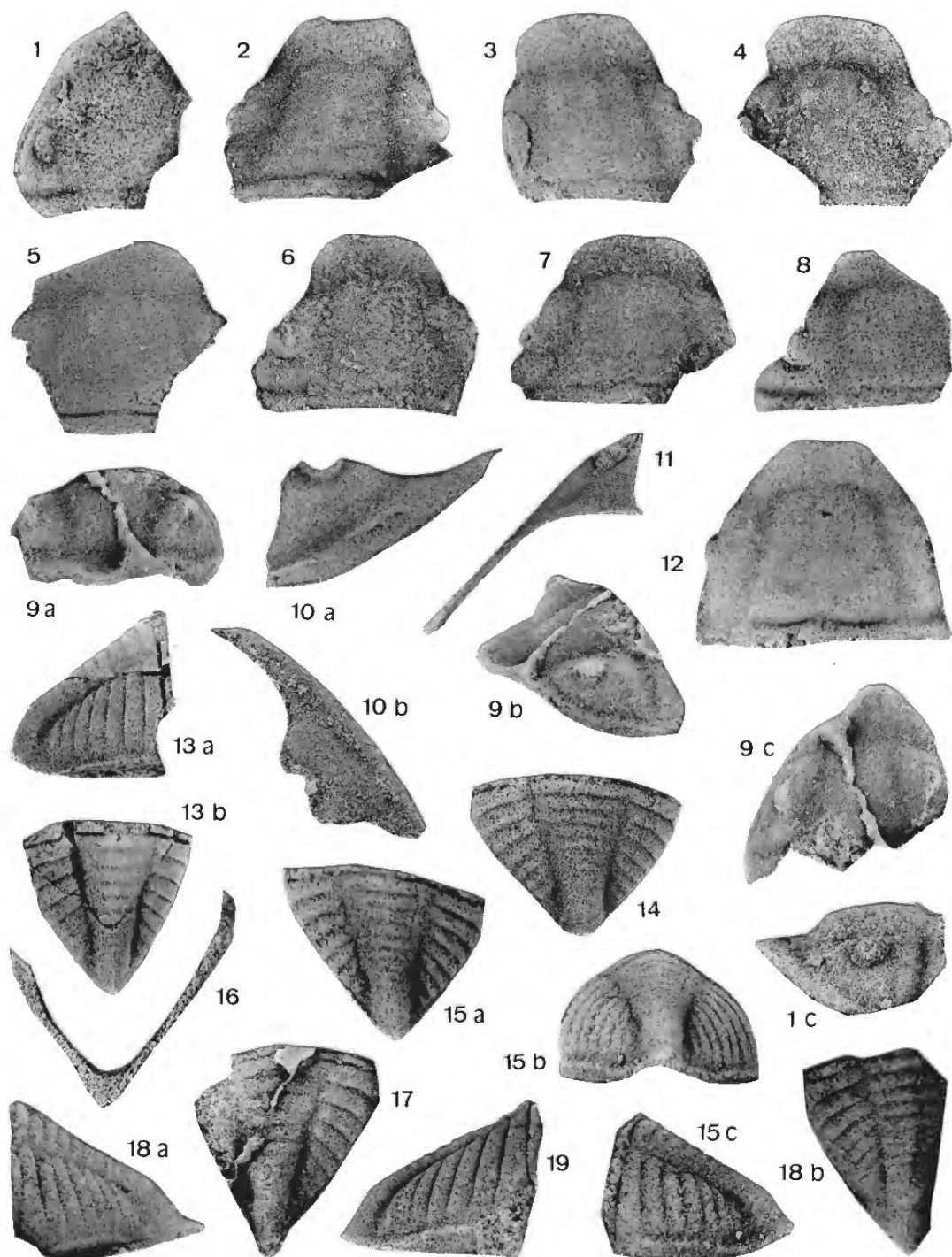
The tricuspid cephalic margin of *Trimerus (Ramiotis) otisi* is comparable to that of *Digonus*, as is the quadrate course of the preocular facial sutures and the very weak expression of the pygidial axial furrows anteriorly, with up to the third rib fused with the axial rings. The species also resembles *Digonus* in the very deep and equally deep pleural and ring furrows. The mod-

erately well defined glabellar lobation and glabellar outline weakly expanded across L1-L1 (tr.) are comparable to early *Digonus* morphologies best represented by *D. zeehanensis*, and in these respects *otisi* is the best candidate as an intermediate species between *Trimerus* and *Digonus*. Significant features precluding the assignment of *otisi* to *Digonus* include the lack of a ventral process on the rostral plate, the very narrow pygidial axis, and the strongly raised postaxial ridge. *T. (R.) otisi* and *Digonus* further differ in the expression of the dorsal sections of the connective sutures (short in *Digonus* but absent in *otisi*), and in the size of the medial cephalic process (small in *Digonus* but very large in *otisi*). In the large size of the medial cephalic cusp, *otisi* is most closely comparable to *T. (T.) johannis*. However, marked differences in cephalic morphology between tricuspid *T. (Trimerus)* (represented by *johannis*), *T. (Ramiotis)* (represented by *otisi*) and *Homalonotus* suggest that the tricuspid cephalic margin was independently derived in these groups.

The paratype cephalon of *Homalonotus vomer* (NMV P12303, Fig. 20.1 and figured Chapman, 1912, pl. 63 fig. 1, Gill, 1949, text-fig. 1B) belongs to *Trimerus (Ramiotis) otisi*, and is designated a paratype of the new species. Chapman (1912) considered the specimen to be a juvenile form of *vomer*, but did not otherwise compare it with the holotype cephalon. Although Chapman's description of *vomer* seems to be based entirely on the holotype, Gill (1949) included features of the paratype in his redescription of the species. Chapman and Gill recorded the localities of the paratype and the holotype of *vomer* only as "Wandong". The holotype was almost certainly collected from PL286 (Williams locality F22, Wandong), where the species occurs in relative abundance and in an identical lithology to that of the holotype. As noted by Gill, the paratype occurs in a yellow-brown, fine grained sandstone. *T. (R.) otisi* has been collected from similar lithologies in the Merriang Syncline to the east of Wandong, and it is presumed the specimen was collected in that area, and probably in the vicinity of PL300, Comet Creek Mine, Clonbinane.

It is remarkable that although *Trimerus (Ramiotis) otisi* is very common in the Eden Park Formation in the Merriang Syncline between Merriang and Clonbinane, trilobites (predominantly homalonotid) are exceedingly rare in the equivalent horizons of the nearby Kinglake Basin sequence.

Figure 20. *Trimerus (Ramiotis) otisi* sp. nov. 1a, paratype NMV P12303 (and paratype of *Homalonotus vomer* Chapman, 1912), cephalon, dorsal view $\times 1.9$ (latex cast) from Wandong (exact locality unknown). 1b, same, $\times 1.7$ (internal mould). 2, paratype NMV P304726, cranidium, dorsal view $\times 2.7$ (latex cast) from PL6633. 3, paratype NMV P304739, incomplete cephalothorax, dorsal view $\times 3.2$ (latex cast) from PL1898. 4, paratype NMV P304797, incomplete cephalothorax, dorsal view of cephalon $\times 2.7$ (internal mould) from PL1898. 5a, holotype NMV P304741, cephalon and displaced thoracopygon, dorsal view of cephalon $\times 1.15$ (internal mould) from PL1898. 5b, same, enlargement of anterior margin $\times 2.3$. 5c, same, anterior view of cephalon $\times 1.15$. 6, paratype NMV P304727, cephalon and displaced thoracopygon, dorsal view of cephalon $\times 2.75$ (internal mould) from PL6633. 7, paratype NMV P304723, cephalon, enlargement of anterior margin $\times 1.6$ (internal mould) from PL6633. 8, paratype NMV P304722, cephalon, enlargement of anterior margin $\times 2.3$ (latex cast) from PL6633. 9a, paratype NMV P304730, cephalon, anterior view $\times 2.1$ (latex cast) from PL6632. 9b, same, oblique view. 9c, same, dorsal view. 10, paratype NMV P304738, thoracopygon, dorsal view $\times 3.0$ (latex cast) from PL1898. 11, paratype NMV P304734, cephalon, dorsal view $\times 4.3$ (internal mould) from PL6632. 12, paratype NMV P304733, cephalon, ventral view (doubleure) $\times 2.0$ (latex cast) from PL6632. 13, paratype NMV P304724, cephalon, ventral view (doubleure) $\times 3.4$ (latex cast) from PL6633. 14a, paratype NMV P304720, pygidium, lateral view $\times 1.9$ (latex cast) from PL6633. 14b, same, dorsal view $\times 1.8$. 15a, paratype NMV P304719, pygidium, dorsal view $\times 1.15$ (latex cast) from PL6633. 15b, same, lateral view. 16a, paratype NMV P304729, pygidium, dorsal view $\times 1.7$ (latex cast) from PL6632. 16b, same, posterior view $\times 1.6$. 17, paratype NMV P304742, pygidium, dorsal view $\times 2.4$ (internal mould) from PL1898. 18, paratype NMV P304737, pygidium, ventral view (doubleure) $\times 1.45$ (latex cast) from PL300. 19, paratype NMV P304718, pygidium, dorsal view $\times 1.4$ (internal mould) from PL6633.



Environmental notes. See taphonomy and biofacies. *Trimerus (Ramiotis) otisi* is considered to have inhabited mid shelf environments.

***Trimerus (Ramiotis) thomasi* sp. nov.**

Figure 21

Trimerus (Dipleura?) sp.—Talent, 1964: 49 (pars), fig. 6 non pl. 26 figs 1–2 (= *Digonus wenndorfi* sp. nov.)

Type material. Holotype NMV P305067 (pygidium) from PL6653, Heathcote, Victoria (Fig. 21.15). Paratypes NMV P305046–P305047 (cephala), NMV P305048, NMV P305053–P305056, NMV P305058, P305059, (cranidia), NMV P305072–P305073 (librigena), NMV P305061, NMV P304063, NMV P305068–P305070, (pygidia) from PL2264, Thomas locality F45, Parish of Heathcote, Heathcote. Paratype NMV P63385 (cranidium), NMV P305043 (pygidium) from PL2265, Thomas locality F46, Parish of Heathcote, Heathcote. For localities see Fig. 8.

Previously figured material. NMV P63385 (ex GSV38132, cranidium, figured Talent, 1964: text–fig. 6) from PL2265.

Registered material. 94 specimens. 3 cephalae, 40 cranidia, 5 librigenae, 1 thoracic segment, 45 pygidia. NMV P305042–P305045, NMV P305127–P305130 from PL2265. NMV P305046–P305053, NMV P305055–P305066, NMV P305068–P305123, NMV P305126 from PL2264. NMV P305124–P305125, NMV P305054, NMV P305067 from PL6653. NMV P305131 from PL6654, Heathcote. NMV P305132 from PL6655, Heathcote. NMV P305133 from PL6656, Heathcote. Unregistered specimens from PL2234, Thomas locality F21, Parish of Heathcote, Heathcote, PL6727, Thomas locality F28, Parish of Redcastle, Heathcote. For localities see Fig. 8.

Stratigraphic distribution. McIvor Formation, ~500 m above the base of the unit, lower *Notoparmella plentiensis* Assemblage Zone, mid Ludlow.

Derivation of name. For Alan T. Thomas (University of Birmingham), for his contribution to the study of homalonotids.

Diagnosis. Cephalon with length about 0.7 times width. Glabella with length equalling width, trapezoid in outline, sides more or less straight, tapering weakly forwards at about 25°. Glabellar lobation distinct, S1–S3 very shallow, L1, L2, L3 and frontal lobe subequal in length (exsag.). Anterior margin of glabella well defined, transverse or with broad medial indentation. Preglabellar field long, 0.25 times cranial length, slightly concave (tr. sect.). Palpebral lobe placed with midline opposite 0.45 cranial length (0.6 glabellar length) and with

δ–δ 1.6 times preoccipital glabellar width. Anterior margin of cranidium transverse to very broadly convex. Pygidium with length equal to width, sides converging at about 70°, angular tip. Pygidial axis wide, 0.43 times pygidial width, continuous with wide, raised postaxial area. 9 distinct axial rings, 7 distinct pleural ribs, axial furrows shallow, pleural furrows moderately impressed, rib-ring offset at fifth-sixth rib.

Remarks. Although specimens are abundant, the quality of the material of *Trimerus (Ramiotis) thomasi* and its similarity to *T. (R.) otisi* does not warrant a full description. The trapezoid, straight-sided and moderately tapered glabellar outline indicate assignment to *Trimerus (Ramiotis)*. The moderate length of the preglabellar field and the weak glabellar lobation are in accord with this assignment. The cranidium figured by Talent (1964: fig. 6) as *T. (Dipleura?)* sp. is significantly larger than cranidia from the type locality of *T. (R.) thomasi* which lies about 500m south-east of PL2265 and more or less on strike. The larger specimen differs conspicuously in that the anterior branches of the facial sutures are more strongly convergent (~70°) and the rostral suture correspondingly shorter (tr.), the preglabellar field is slightly shorter (0.22 cranial length), and the medial flexure of the occipital furrow is strongly expressed (see Fig. 21.12). Whether these differences are attributable to the size or to variability within the species cannot be resolved without further specimens of large individuals. Within the range of intraspecific variability, there are specimens of *thomasi* exhibiting very weak lobation, and short and more strongly tapered glabellar outlines (e.g. Figs 21.4, 21.5). These morphs are closely comparable to the contemporary *T. (R.) salteri* from England. Original illustrations of the holotype [Salter, 1865: pl. 12 fig. 1, as *Homalonotus (Koenegia) ludensis*] indicates that the English species differs from *thomasi* in having a wider (tr.) preocular fixigenal field and deeper axial furrows.

Trimerus (Ramiotis) permutus from the upper Ludlow of Poland is close in age to *T. (R.) thomasi*. In cephalic morphology *permutus* differs markedly from *thomasi* in exhibiting strong glabellar lobation, an elongate glabellar outline, more strongly convergent facial sutures, and a short preglabellar field. The species are more closely comparable on pygidial features. Although pygidia of *permutus* are poorly known, they share with *thomasi* the elongate pygidial proportions and moderately and equally impressed axial, pleural and ring furrows.

Figure 21. *Trimerus (Ramiotis) thomasi* sp. nov. 1, paratype NMV P305046, cephalon, dorsal view × 2.5 (internal mould) from PL2264. 2, paratype NMV P305048, cranidium, dorsal view × 2.5 (latex cast) from PL2264. 3, paratype NMV P305055, cranidium, dorsal view × 2.6 (internal mould) from PL2264. 4, paratype NMV P305059, cranidium, dorsal view × 2.4 (latex cast) from PL2264. 5, paratype NMV P305053, cranidium, dorsal view × 2.7 (internal mould) from PL2264. 6, paratype NMV P305056, cranidium, dorsal view × 2.9 (latex cast) from PL2264. 7, paratype NMV P305054, cranidium, dorsal view × 2.6 (latex cast) from PL6653. 8, paratype NMV P305058, cranidium, dorsal view × 2.6 (latex cast) from PL2264. 9a, paratype NMV P305047, cephalon, anterior view × 2.3 (latex cast) from PL2264. 9b, same, oblique view × 1.8. 9c, same, dorsal view × 2.4. 10a, paratype NMV P305072, librigena, lateral view × 2.0 (internal mould) from PL2264. 10b, same, dorsal view (latex cast). 11, paratype NMV P305073, librigena, ventral view (double) × 1.7 (latex cast) from PL2264. 12, NMV P63385, cranidium, dorsal view × 1.95 (internal mould) from PL2265. 13a, paratype NMV P305068, pygidium, lateral view × 1.9 (internal mould) from PL2264. 13b, same, dorsal view. 14, paratype NMV P304063, pygidium, dorsal view × 3.0 (internal mould) from PL2264. 15a, holotype NMV P305067, pygidium, dorsal view × 3.0 (internal mould) from PL6653. 15b, same, posterior view. 15c, same, oblique view. 16, paratype NMV P305070, pygidium, ventral view × 4.0 (internal mould) from PL2264. 17, paratype NMV P305061, pygidium, dorsal view × 2.5 (latex cast) from PL2264. 18a, paratype NMV P305043, pygidium, lateral view × 2.4 (latex cast) from PL2265. 18b, same, dorsal view × 2.5. 19, paratype NMV P305069, pygidium, lateral view × 3.2 (internal mould) from PL2264.

The pygidia differ in that *thomasi* exhibits a markedly raised postaxial ridge, whilst that of *permutus* is low.

Trimerus (Ramiotis) otisi from southern central Victoria is another contemporary of *T. (R.) thomasi*. Despite their geographic and temporal proximity, *otisi* and *thomasi* can be easily distinguished. The pygidia of *thomasi* are much more elongate, have a wider axis, and exhibit shallower pleural and ring furrows and deeper axial furrows. The cranidia of *thomasi* generally exhibit a more straight-sided and shorter glabellar outline, more weakly defined glabellar lobation, and a longer preglabellar field. Despite these differences, *otisi* and *thomasi* are considered to be closely related. Together with the poorly known *T. (R.)* sp. A from Bolivia, the species share a distinct pygidial morphology including pleural furrows that continue to a deep border furrow, and a raised ridge-like border. This pygidial morphology distinguishes this species group from Llandovery-Wenlock *T. (Ramiotis)*. In other respects *T. (R.)* sp. A is morphologically intermediate between *otisi* and *thomasi*, exhibiting longer pygidial proportions of the latter and deeper pygidial pleural and ring furrows of the former.

Of the Llandovery-Wenlock species of *Trimerus (Ramiotis)*, *T. (R.) thomasi* shows greatest resemblance to *T. (R.) tomczykowae* from the Wenlock of Victoria (described below), that also exhibits very weak lobation, a transverse rostral suture, shorter glabellar proportions and a long preglabellar field. The species also share moderate and subequal depth of the pygidial pleural and ring furrows, distinguishing them from other Llandovery-Wenlock *T. (Ramiotis)*. *T. (R.) tomczykowae* differs in having a short, rounded pygidial outline, slightly longer glabellar proportion, and a deep medial indentation of the glabellar anterior margin.

Environmental notes. *Trimerus (Ramiotis) thomasi* is the dominant element of monospecific or low diversity assemblages. Three cephalons from PL2264 are the only known articulated specimens, isolated tergites representing 97% of the entire population, typical of taphofacies TII. The species occurs in medium-grained sandstones, associated with a shelly fauna dominated by gastropods and brachiopods. *T. (R.) thomasi* is considered to have inhabited inner shelf environments.

***Trimerus (Ramiotis) tomczykowae* sp. nov.**

Figures 19.5, 19.8, 19.10, 19.12

Type material. Holotype NMV P138203 (pygidium) from the “*Illaeus* band”, Costerfield, Victoria (Fig. 19.8). Paratype NMV P305191 (cranidium) from PL2263, Thomas locality F44, Parish of Dargile, Costerfield. Paratypes NMV P138292, P138293 (rostral plates) from PL1460, Thomas locality F43A, Parish of Dargile, Costerfield. For localities see Fig. 10.

Registered material. 8 specimens: 1 cephalon, 3 cranidia, 2 rostral plates, 2 pygidia. NMV P138291–P138294, NMV P138296, NMV P139358 from PL1460. NMV P305191 from PL2263. NMV P138203 from the “*Illaeus* band”.

Stratigraphic distribution. *Illaeus* band, Wapentake Formation. Rickards and Sandford (1998) interpreted *Ananaspis typhlagogus* to indicate a Wenlock age for these beds.

Derivation of name. For Ewa Tomczykowa (Instytut

Geologiczny, Poland) for her contribution to the study of homalonotids.

Diagnosis. Glabella trapezoid, elongate, length ~1.1 times width, sides parallel opposite paraglabellar area, straight and converging at about 20° anteriorly, with extremely weak lobation, anterior margin strongly indented. Paraglabellar area distinct. Palpebral lobe placed at about 0.55 glabellar length. Rostral suture more or less transverse. Dorsal surface of rostral plate long, one third length of ventral surface, anterior margin of rostral plate with sides converging at 115°, rounded medially. Connective sutures straight, diverging forwards at 55°. Ventral surface of rostral plate flat, length equalling width. Pygidial axial furrows moderately impressed. Axis about 0.4 times pygidial width, sides straight and tapering at 25°, posterior third of axis moderately convex and raised, terminal piece continuous with and not distinguishable from wide, raised, subparallel-sided postaxial ridge. 10 axial rings, ring furrows moderately impressed, 7 pleural ribs, pleural furrows moderately impressed and equal in depth to ring furrows, shallowing distally. Pleural offset at fourth rib.

Discussion. *Trimerus (Ramiotis) tomczykowae* is a very rare element of the *Illaeus* band fauna. Despite the very few and fragmentary specimens available, a fairly complete reconstruction of the cephalon can be made, and together with the single, well-preserved pygidium clearly represents a new species of homalonotid and a full description of the species is possible with the material at hand. Significant cephalic characters include the elongate, trapezoid, straight-sided, moderately tapering glabella, the weakly expressed glabellar lobation, the moderate length of the preglabellar field (0.25 cranial length) and the short pygidial proportions (L/W~0.9) indicate assignment to *T. (Ramiotis)*. In cephalic features *tomczykowae* differs from the type species *T. (R.) rickardsi* in having a transverse rostral suture and strong medial indentation of the anterior glabellar margin. In these respects *tomczykowae* is closest to *T. (R.) dyaulax*.

The equal depth of pleural and ring furrows attained by *Trimerus (Ramiotis) tomczykowae* is considered here to represent a significant stage of homalonotine development. This feature distinguishes Wenlock-Ludlow *T. (Ramiotis)* from Llandovery members of the group. Although in its short pygidial proportions and rounded outline the affinities of *tomczykowae* to Llandovery *T. (Ramiotis)* are clear, it represents a transitional morphology between these and Upper Silurian species of *T. (Ramiotis)* and *T. (Trimerus)*.

Indeterminate homalonotids from the Wenlock of central Victoria include a partly disarticulated exoskeleton from the old Toorong Brick Pit, high in the Anderson Creek Formation, only briefly examined by the author. The abundant and diverse trilobite fauna occurring in the Bylands Siltstone at PL206, Wallan has yielded only an single homalonotid thoracic segment.

Environmental notes. *Trimerus (Ramiotis) tomczykowae* is a very rare element of a moderately diverse fauna occurring in the nodular mudstones of the *Illaeus* band. The fauna is dominated by the blind illaenid *Thomastus thomastus* Öpik, 1953.

Together with *Anaspis typhlagogus* the composition of the fauna closely resembles a contemporary fauna from Argentina described by Waisfeld and Sanchez (1993). The taphonomy of the *Illaeus* band is characterised by an abundance of complete exoskeletons of *Thomastus* in the 'bumastoid stance', presumed to be individuals preserved in their infaunal life position (Sandford and Holloway, 1998). The taphonomy and the autecology of *Thomastus* in the mudstones suggest a deeper water environment for *tomczykowae*. Several specimens of *tomczykowae* occur in a richly fossiliferous sandstone presumably interbedded within the mudstone, although the bed is not known in outcrop.

Wenndorfia gen. nov.

Type species. *Homalonotus mutabilis* Koch, 1880 from the Lower Devonian (upper Emsian) of Germany.

Other species included. *Parahomalonotus angusticostatus* Tomczykowa, 1975, *P. bostoviensis* Tomczykowa, 1975, *Digonus elegans* Tomczykowa, 1975, *Homalonotus expansus* Hector, 1876 (= *H. (Burmeisteria) huttoni* Allan, 1935, = *D. margaritifera* Wenndorf, 1990), *H. forbesi* Rouault, 1855, *Dipleura fornix* Haas, 1968, *Trimerus lilydalis* Gill, 1949, *H. miloni* Renaud, 1942, *H. multicostatus* Koch, 1883a, *H. mutabilis* Koch, 1880, *T. novus* Tomczykowa, 1975, *H. obtusus* Sandberger and Sandberger, 1849, *P. planus junior* Wenndorf, 1990, *H. planus* Sandberger, 1849, "*P. sp. nov. A*" in Wenndorf, 1990, "*D. sp.*" in Le Menn et al., 1976.

Range. Lower Devonian (Lochkovian-Emsian).

Diagnosis. Glabella of moderate height to very low, weakly tapering. Lobation indistinct. Anterior margin of cranium U-shaped and more or less concentric with rounded anterior margin of glabella, anterior branches of facial suture broadly curved and strongly convergent anteriorly, rostral suture short (tr.), transverse or continuous in curvature with anterior section of facial suture. Eyes placed posteriorly, opposite 0.3–0.45 cephalic length. Sides of glabella more or less straight and parallel, varying to strongly concave. Ventral surface of rostral plate with low or prominent anterior node. Pygidial outline parabolic with rounded tip, but triangular with pointed tip in early species. Pygidium with axial furrows very shallow to indistinct, axis without independent convexity, wide (0.4–0.65 time pygidial width anteriorly), strongly tapering (furrows converging at 30–45°), not reaching margin but terminating at about 0.85–0.95 times pygidial length, semicircular terminal piece short (sag.), slightly raised, but often indistinct from postaxial field.

Discussion. *Wenndorfia* has been erected to accommodate many species previously assigned to *Parahomalonotus* (see above). In establishing *Parahomalonotus*, Reed (1918) listed a number of characters in the diagnosis that are not apparent in the type species *Homalonotus gervillei* DeVerneuil, 1850 from the Emsian of France. Reed described the "*facial sutures uniting in a regular wide arched commissure close to (the) anterior margin*" as diagnostic of the genus (Reed, 1918: 326). However, in *gervillei* the anterior cranial margin is quadrate, the rostral suture being transverse and the anterior branches of the facial sutures subparallel (see Pillet, 1973: fig. 120). Reed's

original diagnosis also states a pygidial entire margin and more or less indistinct trilobation as diagnostic. However, in contradiction to these definitive parameters, trilobation is well defined by the raised pygidial axis of *gervillei*, and the postaxial ridge extends posteriorly as a short posteromedial spine (see Pillet, 1973, pl. 37 fig. 5).

The revised diagnosis for *Parahomalonotus* s.s. (see above) emphasises the distinctive features of *P. gervillei*, and hence differs markedly from that given by Reed (1918). Of species assigned to *Wenndorfia*, Reed assigned *Homalonotus planus*, *H. obtusus* and *H. multicostatus* to *Parahomalonotus* with question. In the course of their facial sutures and in pygidial features, these species are in closer agreement with Reed's diagnosis of *Parahomalonotus* than with the type *gervillei*. These species further differ from *gervillei* in having pygidial axes that are much wider anteriorly, taper more strongly, are not independently convex, lack postaxial ridges, and terminate between 0.85 and 0.95 pygidial length, and glabellae that are very low and lack distinct lobation.

Species included in *Wenndorfia* were previously assigned variously to *Digonus*, *Dipleura*, *Parahomalonotus* and *Trimerus*. *Wenndorfia* is most reliably distinguished from these genera by the rounded outline of the anterior cranial margin, concentric to the strongly rounded glabellar anterior margin. This morphology contrasts most strongly with the angular, quadrate anterior cranial margin of *Digonus*. In pygidial morphology early representatives of *Wenndorfia* and *Digonus* are alike, although marked differences between these groups are manifest in later representatives in trends toward short, rounded outlines, and elongate, triangular outlines with acute processes respectively. Later representatives of *Wenndorfia* further differ from *Digonus* in exhibiting moderately to strongly concave glabellar sides.

Rostral morphology is recognised in this work as a reliable character distinguishing *Wenndorfia* from *Trimerus* and *Dipleura*. The rostral plate of *Wenndorfia* exhibits a diamond-shaped outline and exhibits a variably developed antero-medial node, whereas rostral plates of *Trimerus* and *Dipleura* are elongate pentangular and pentangular in outline respectively, and lack rostral processes.

Developmental trends in the pygidial morphology of *Wenndorfia*, manifest in the replacement of triangular outlines by rounded outlines in the mid-Pragian, are comparable to developmental trends in *Dipleura* in the Late Silurian. However, pygidia of species assigned to *Wenndorfia* vary markedly in the depth of the pleural and ring furrows. In a number of species the pleural and ring furrows are very shallow to indistinct, and approach morphologies exhibited by species of *Dipleura*. The distinction of these morphologically convergent species relies on the course of the cephalic sutures, as discussed above (see *Dipleura*). Pygidia of *Trimerus* (*Ramiotis*) and *T. (Trimerus)* are distinguished from the *Wenndorfia* pygidial morphology in having a distinct postaxial ridge.

Wenndorfia mutabilis, unlike most other species of the genus, is abundant and its dorsal and ventral morphology is both completely known and recently redescribed (see Wenndorf, 1990). The species exhibits the rounded anterior cranial margin, the weakly expressed pygidial trilobation and

the entire pygidial margin included in Reed's original diagnosis of *Parahomalonotus* and in the diagnosis of *Wenndorfia*. Other features exhibited by *mutabilis* and considered typical of *Wenndorfia* include the strongly rounded anterior margin of glabella, the posteriorly placed eyes, the small node on the ventral surface of rostral plate, and the wide, strongly tapering axis terminating at about 0.85 pygidial length. *W. mutabilis* is distinguished from its congeners in having a glabella of moderate height with strongly concave sides, a wide palebral area, and a shorter pygidial outline with shallow pygidial ring and pleural furrows.

Lochkovian-lower Pragian *Wenndorfia* differ from upper Pragian-Eifelian species in variously exhibiting features that can be regarded as underived. These features include a trapezoid glabellar outline, the expression of glabellar lobation, moderately impressed pygidial axial furrows, deep pleural and ring furrows, and a triangular pygidial outline with an obtusely angled tip. In these respects these early species represent a transitional morphologies with early *Digonus*. Early representatives of *Wenndorfia* include several Polish homalonotids originally described as species of *Digonus* by Tomczykowa (1975) and regarded by Wenndorf (1990) as representing an early *Digonus* morphology. Lacking in these Polish species is the quadrate anterior cranial outline exhibited by the earliest *Digonus* (see above, *D. wenndorfi*). The strongly rounded anterior glabellar margin, the concentric cranial margin and posteriorly placed eyes indicate assignment of these species to *Wenndorfia*. The upper Lochkovian *W. bostoviensis* from Poland is the earliest species assigned to *Wenndorfia*. *W. bostoviensis* differs from *W. mutabilis* and other *Wenndorfia* in having and a short triangular pygidial outline. This pygidial morphology suggests affinities of the earliest *Wenndorfia* to the earliest *Digonus*.

Tomczykowa (1975) assigned homalonotids from upper Lochkovian-lower Pragian strata immediately overlying *Wenndorfia bostoviensis* to *Digonus vialai*. The number of specimens representing these two morphologies is limited, with four cranidia representing *vialai* and two representing *bostoviensis*. Tomczykowa distinguished *vialai* from *bostoviensis* by its trapezoid rather than rectangular glabellar outline, but the significance of these supposed differences cannot be determined without reference to larger populations. In all other

respects it is difficult to distinguish *vialai* from *bostoviensis*, and the specimens are best considered conspecific. Similarly, Tomczykowa described *Parahomalonotus angusticostatus* from the lower Pragian of Poland using a limited collection of pygidia, only one complete. Tomczykowa (pl. 6 figs 1–4) assigned pygidia from a slightly lower horizon to *Parahomalonotus forbesi* (Rouault, 1855), distinguished from those of *angusticostatus* in having fewer axial rings and ribs and shallower pleural and ring furrows. However, the pygidia figured do not differ markedly from *angusticostatus* and are considered to be conspecific.

Wenndorfia expansa (Hector, 1876)

Figure 22.7–22.14

Homalonotus expansus Hector, 1876: 602, pl. 27 fig. 2.

Homalonotus sp.—Hutton, 1888: 257.

Homalonotus (*Burmeisteria*) *huttoni*.—Allan, 1935: 28, pl. 1 figs 4–5.

Homalonotus (*Digonus*) *expansus*.—Allan, 1935: 29, pl. 1 fig. 1.

Homalonotus (*Digonus*) cf. *expansus*.—Allan, 1935: 29, pl. 1 fig. 3.

Burmeisteria (*Digonus*) *expansus*.—Saul, 1965: 271.

Burmeisteria huttoni.—Saul, 1965: 271.—Tomczykowa, 1975: 11.

Digonus expansus.—Tomczykowa, 1975: 11.—Wenndorf, 1990: 16.

Burmeisteria (*Digonus*) cf. *expansus*.—Speden and Keyes, 1981: pl. 4 fig.1.

Burmeisteria expansa.—Cooper, 1982: 27.

Burmeisteria huttoni.—Cooper, 1982: 27.—Wenndorf, 1990: 16.

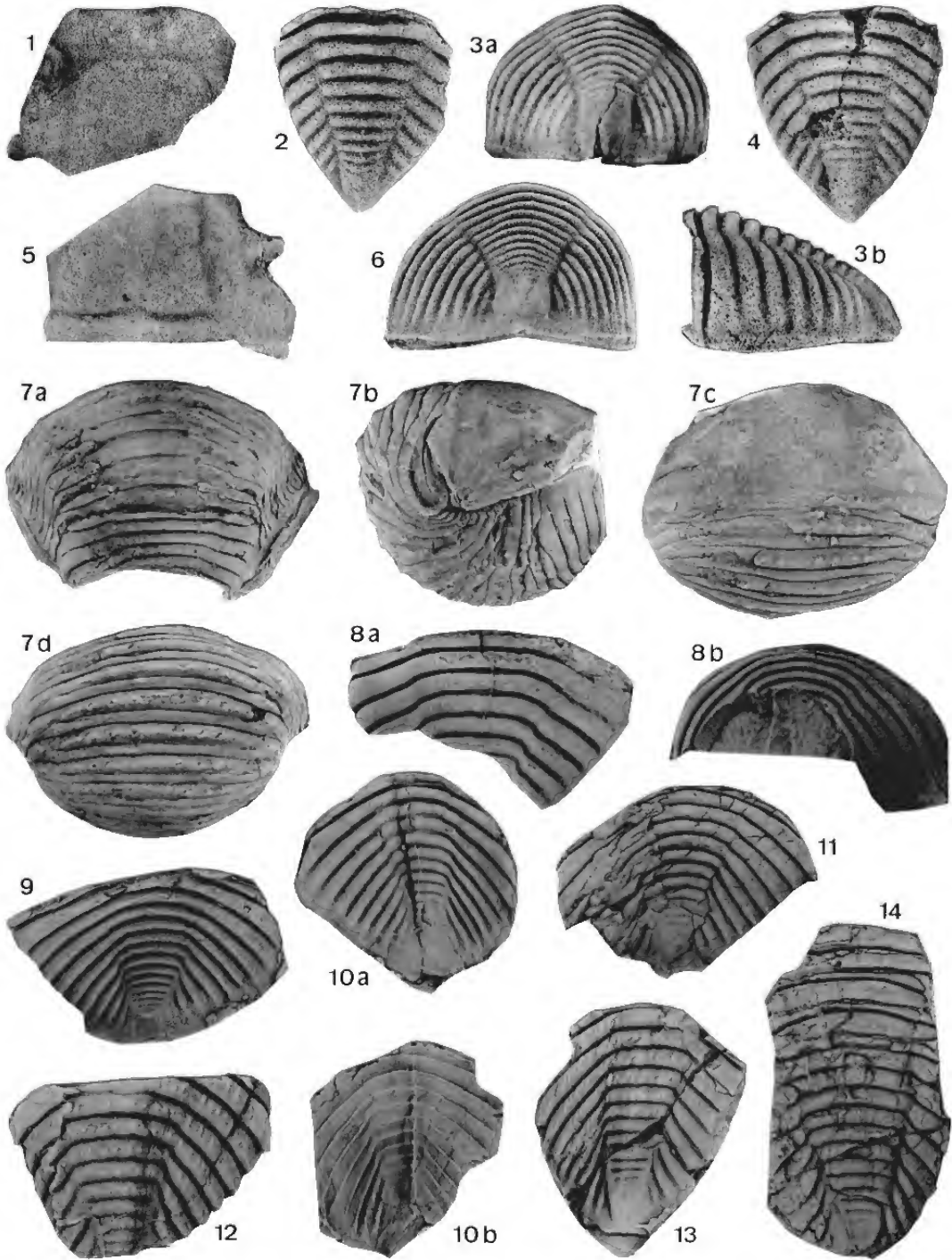
Digonus margaritifera —Wenndorf, 1990: 77, pl. 11 figs 8–9.

Type material. *Homalonotus expansus*. Lectotype (pygidium, figured Hector, 1876, Allan, 1935: pl. 1 fig. 1, Fig. 22.10 herein, in the Geological Survey of New Zealand, cast in Museum Victoria registered NMV P16844) from McKay locality 129, Rainy Creek, Reefton, south island, New Zealand. Paralectotype (pygidium, also the holotype of *Digonus margaritifera*, figured Allan, 1935: pl. 1 fig. 3, Wenndorf, 1990: pl. 11 fig. 8, in the Geological Survey of New Zealand, cast in Museum Victoria registered NMV P16846) from McKay locality 130, Lankey Gully, Reefton. Paralectotype (pygidium, figured Hector, 1876, in the Geological Survey of New Zealand, cast in Museum Victoria registered NMV P16847) from locality 129.

Homalonotus (*Burmeisteria*) *huttoni*. Holotype ZFc33 (dorsal exoskeleton, figured Allan, 1935: pl. 1 figs 4, 5) from “near Reefton”. Allan (1935) suggested the specimen is from locality 129.

Figure 22.1–22.6. *Digonus wenndorfi* sp. nov. 1, paratype NMV P304713, cranidium, dorsal view $\times 1.4$ (internal mould) from PL2203. 2, paratype NMV P304862, pygidium, dorsal view $\times 1.5$ (internal mould) from PL2203. 3a, paratype NMV P304864, pygidium, posterior view $\times 1.35$ (internal mould) from PL2203. 3b, same, lateral view $\times 1.25$. 4, paratype NMV P304866, pygidium, dorsal view $\times 1.25$ (internal mould) from PL2203. 5, paratype NMV P304710, cranidium, dorsal view $\times 1.0$ (internal mould) from PL2203. 6, paratype NMV P304717, pygidium, posterior view $\times 1.15$ (internal mould) from PL2203.

Figure 22.7–22.14. *Wenndorfia expansa* (Hector, 1876). 7a, holotype of *Homalonotus* (*Burmeisteria*) *huttoni* Allan, 1935, ZFc 33, enrolled exoskeleton, dorsal view of pygidium $\times 0.7$ (internal mould) from near Reefton (exact locality unknown). 7b, same, lateral view of enrolled exoskeleton. 7c, same, dorsal view of cephalon. 7d, same, posterior view of enrolled exoskeleton. 8a, NMV P64122, pygidium, dorsal view $\times 0.9$ (internal mould) from “Reefton”. 8b, same, posterior view. 9, paralectotype of *Homalonotus expansus* Hector, 1876 and holotype of *Digonus margaritifera*, pygidium, dorsal view $\times 0.9$ (internal mould) from locality 130, Reefton (NMV P16846, plastercast of original). 10a, lectotype of *Homalonotus expansus* Hector, 1876, pygidium, dorsal view $\times 1.15$ (internal mould) from locality 129, Reefton (NMV P16844, plastercast of original). 10b, same, external mould. 11, paralectotype of *Homalonotus expansus* Hector, 1876, pygidium, dorsal view $\times 0.7$ (internal mould) from locality 129, Reefton (NMV P16847, plastercast of original). 12, NMV P64121, pygidium, dorsal view $\times 1.23$ (internal mould) from “Reefton”. 13, NMV P64120, pygidium, dorsal view $\times 0.95$ (internal mould) from “Reefton”. 14, ZFc 58, incomplete thoracopygon, dorsal view $\times 0.75$ (internal mould) from “Reefton”.



Digonus margaritifera. Holotype (pygidium, and paralectotype of *Homalonotus expansus*, see above). Paratype (pygidium, figured Wenndorf, 1990: pl. 11 fig. 9, in the Paläontologisches Museum der Humboldt-Universität Berlin, Germany), documented as coming from Kilmore, Victoria, acquired through the fossil dealer Kranz in 1885. However as the paratype is undoubtedly conspecific with the New Zealand material, as no homalonotids other than *Trimerus* (*Trimerus*) *vomer*, *Trimerus* (*Ramiotis*) *otisi* and *Dipleura garratti* are yet known in the well-collected Wenlock-Ludlow trilobite faunas from the Kilmore area, and as *Wenndorfia* would be most unexpected in strata of this age, I conclude that the Berlin specimen is from the Reefton area and its documentation confused, possibly by Kranz, with a specimen of *T. (T.) vomer*. Kranz may have acquired the Berlin specimen from Theodore Ranft who was the first to collect fossils in Lankey Gully at Reefton in 1872. Part of Ranft's collection was purchased by the Melbourne Museum, who also had dealings with Kranz.

Previously figured material. NZGS AR 676 (thoracopygon, figured Speden and Keyes, 1981: pl. 4 fig. 1) from locality GS3737, S38/f523, Rainy Creek, Reefton.

Registered material. 12 specimens: 1 complete exoskeleton, 2 thoracopygons, 1 incomplete thorax, 8 pygidia., NMV P16844, NMV P16847 from locality 129, P16846 from locality 130. NZGS AR676 from locality GS3737. NMV P64120–P64122 from Lankey Gully (Ranft collection). ZFc33, ZFc58, ZFc309, ZFc350 from "Reefton". One pygidium in the Paläontologisches Museum der Humboldt-Universität Berlin.

Stratigraphic distribution. Lankey Limestone, ?*Boucotia loyolensis* Assemblage Zone, Emsian.

Diagnosis. Glabella extremely low, sides parallel, without distinct lobation, anterior margin broadly rounded, length 1.1 times width. Palpebral lobes placed opposite ~0.55 glabellar length. Axial furrows very poorly defined. Pygidium short, with length 0.7 times width, weakly concave sides, converging posteriorly at about 100° to an obtusely angular tip. Pygidial axis wide, about 0.4 times pygidial width and very poorly defined anteriorly, tapering moderately with sides straight and converging at about 30°, length about 0.85 times pygidial length, posterior margin parabolic, 12–13 rings, semicircular terminal piece with distinct posterior margin. Axial furrows poorly defined, indicated by flexure of pleurae, almost indistinct anteriorly. 9 pleural ribs. Pleural furrows not reaching margin. Pleural and ring furrows deep and of equal depth. Anteriorly ribs and rings continuous, pleural offset at seventh rib. Row of equidimensional, regularly spaced tubercles on axial area of thoracic and pygidial segments, with two or three supplementary rows of smaller tubercles. Tubercles large on larger specimens, small to fine on smaller specimens. Similar, but less regular tuberculation on posterior border of fixigenae and thoracic and pygidial pleurae. Genal field with densely spaced, coarse granules.

Discussion. Three homalonotids have been named from the Lower Devonian at Reefton. The best known of these is *Homalonotus* (*Burmeisteria*) *huttoni*, based on a single, near-complete, enrolled exoskeleton (Fig. 22.7). The specimen was described in detail in open nomenclature by Hutton (1888), and later named by Allan (1935). Several points in Hutton's original description of the specimen cannot be substantiated, in

particular those concerning the cephalic shape and proportions, and the presence of distinct glabellar lobation. Although only the first six segments of the pygidium are preserved in the holotype, the ornament of tubercles on the pleural ribs and axial rings are distinctive and shared by several more completely preserved pygidia in the Museum of Victoria (NMV P64120–2, Figs 22.8, 22.12–22.13) and in the New Zealand Geological Survey (NZGS AR 676, Fig. 22.14). These pygidia also share very deep ring and pleural furrows that are continuous to the seventh segment. The axial furrow is not impressed on the anterior half of the pygidium, but its position is indicated by a posteriorly increasing flexure at the junction of the ring and pleural furrows. These specimens are considered to be conspecific with the holotype of *huttoni*.

The other two species, *Homalonotus expansus* and *Digonus margaritifera*, were based only on pygidia. Wenndorf's (1990) description of *margaritifera* includes features identical with those of *H. (Burmeisteria) huttoni*, such as the ornament, the deep axial ring and pleural furrows continuous to the seventh rib, the very shallow axial furrows, and the wide rounded-triangular outline. Wenndorf noted *expansus* and *margaritifera* shared pleural offsetting at the seventh-eighth rib, but distinguished the former by the smooth surface texture (absence of tubercles) and the weak definition of the axis of the former species. Close inspection of the external mould of the lectotype of *expansus* reveals, however, a row of small tubercles on the first four axial rings and pleurae (see Fig. 22.10b). Corresponding ornament on the anteriormost rings on the internal mould were not recorded either by Hector (1876) or by Allan (1935) as this area of the pygidium is damaged. The spacing of these tubercles on the lectotype is similar to that of *huttoni*. The differences in the coarseness of tuberculation between the type specimens of *expansus* and specimens of *huttoni* are attributed here to the size of the pygidia. The lectotype of *expansus*, with the finest tubercles, is the smallest specimen. Moderately sized specimens including the holotype of *margaritifera* have slightly larger tubercles (see Fig. 22.9), whereas the largest of specimens including the holotype of *huttoni* have much larger tubercles. This interpretation is in accord with Cooper's (1982) suggestion that *expansus* and *huttoni* might be synonyms. The differences in definition of the axis between *margaritifera* and *expansus* noted by Wenndorf (1990) can be attributed to the flattening of the lectotype of *expansus*, axial convexity obscured by crushing and longitudoinal folding of the tergite. Taking this deformation into account, whatever differences may have existed between the specimens do not appear to be significant. In the absence of significant differences in ornament or other features between the types of *expansus* and pygidia of *margaritifera* and *huttoni*, the species are regarded as conspecific.

There is little to support the assignment of *Homalonotus expansus* to *Burmeisteria*. The most reliable character of *Burmeisteria* recognised in this work is the exceptionally high number of pygidial segments, with *B. herschellii* having up to 17 axial rings and 11 pleural furrows. *H. expansus* has only 12 axial rings and 9 pleural ribs. Reed (1918) emphasised the biconcave course of the rostral suture in *herschellii* as a generic

character. Cooper (1982) suggested the course of the rostral suture of *herschelii* to be variable and probably ontogenetically related, supporting earlier doubts on its significance (Sdzuy, 1957, Saul, 1965). Notwithstanding this debate, the anterior portion of the cephalon (and the rostral suture) of the holotype of *huttoni* is not preserved. *B. herschelii* is strongly polymorphic, with variable glabellar morphology, but the glabella of *expansus* differs in having no trace of lobation or spines, and in that the axial furrows are subparallel and much shallower. In the absence of rostral morphology, the assignment of *huttoni* to *Burmeisteria* by various workers (Allan, 1935, Wenndorf, 1990) was presumably based on the similarity of the tuberculate ornament to that of *herschelii*. The arrangement of these tubercles suggests, however, they are not homologous, but independently derived. As noted by Cooper (1982), the tubercles of *herschelii* are arranged longitudinally. This arrangement differs from the transversely arranged tubercles on *expansus*.

Tuberculation similar to that exhibited by *Homalonotus expansus* is known amongst members of *Digonos*. Wenndorf (1990) noted a close similarity in pygidial ornament between the paratypes of *margaritifera* and the *ornatus* group. Wenndorf added that *margaritifera* shared few other *ornatus*-group characters. The narrow pygidial axis is incompatible with assignment of *expansus* to *Digonos*.

Generic assignment of *Homalonotus expansus* to *Wenndorfia* emphasises its low glabellar height, rounded anterior glabellar margin, posteriorly placed eyes, indistinct pygidial axial furrows and narrow axial width, and the continuity of the ring and pleural furrows, the termination of the axis at about 0.9 pygidial length, and the absence of a postaxial ridge. Its relationships to other species of *Wenndorfia* are difficult to assess, but it differs from all other species in exhibiting a coarsely tuberculate thoracic and pygidial ornament. In overall appearance, pygidia assigned to *W. expansus* most closely resemble the deeply furrowed pygidia of *W. multicosata*. The triangular pygidial outline, however, distinguishes it from *multicosata* and most other *Wenndorfia*, as discussed above. As the cephalic morphology of *multicosata* is poorly known, it is difficult to make a detailed comparison with *expansus*. The very low height and poor definition of the glabella of *expansus* is approached only by *W. plana plana*, although the latter differs in that the glabellar axial furrows are quite distinct posteriorly.

Shirley (1938) recorded *Homalonotus* sp. from the Baton Formation at Baton River, east of Nelson, North Island, New Zealand. He considered ten crushed and deformed pygidia to be identical with pygidia of *Wenndorfia expansus*. Shirley's description of the number of axial rings and pleural ribs and the continuity of the rings and pleurae are in accord with *expansus*, but as I have not examined these specimens I can make no judgement on their affinities. The Baton Formation is generally considered younger than the Lankey Limestone at Reefton, although its age is variably cited as Pragian (Boucot et al., 1969) or Lochkovian (Wright, 1990).

The newly documented material warrants a revised diagnosis of the species, but otherwise is too limited to warrant a complete description to replace those of Hutton (1888), Allan (1935) and Wenndorf (1990).

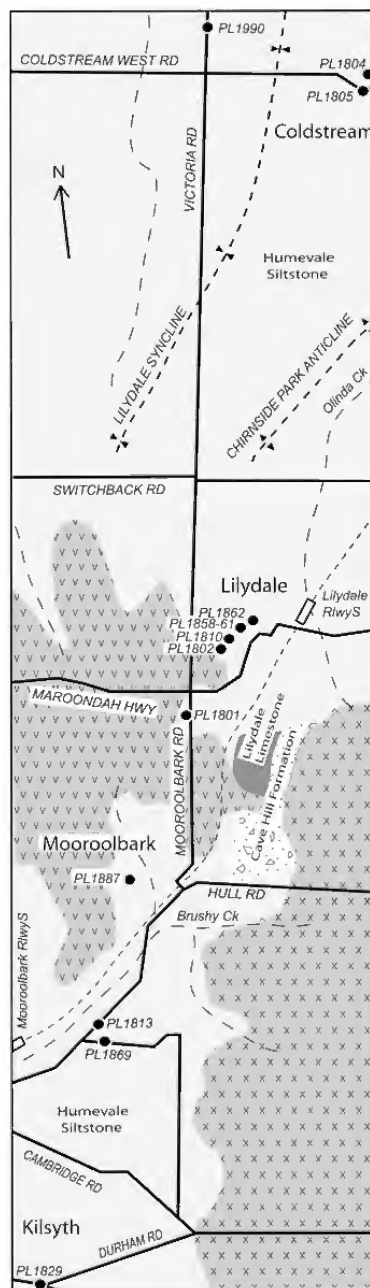


Figure 23. Geological sketch map of the Lilydale area showing Lochkovian-basal Pragian fossil localities yielding homalonotids. For other fossil localities see also Gill (1940, fig.1, 1945, fig. 2), Moore (1965, fig.1), VandenBerg (1970), Garratt (1972), Wall et al. (1995, fig. 1), Sandford (2003, text-fig. 1A, 2004, fig. 1).

Environmental notes. The taphonomy of the population of *Wenndorfia expansa* (as a whole) are attributable to Speyer and Brett's taphofacies 4B, with Ar=33% and the relative abundance of completely enrolled specimens (8%). *W. expansa* is interpreted to inhabit deep, outer-shelf environments. This suggested habitat is comparable to the deepest water facies associated with populations of many other species of *Wenndorfia* (see Wenndorf, 1990)

***Wenndorfia lilydalensis* (Gill, 1949)**

Figures 5C, 24

Homalonotus harrisoni.—Cresswell, 1894: 156.

Homalonotus sp.—Chapman, 1907: 239.—Gill, 1938: 170.

Trimerus lilydalensis Gill, 1949: 69, pl. 8 figs 4–5, pl. 9 fig. 7, text-fig. 1F—Holloway and Neil, 1982: 145.

Type material. Holotype NMV P14587 (cephalon, figured Gill, 1949: pl. 8 figs 4–5, text-fig. 1F, Fig. 24.1 herein, counterpart previously registered NMV P14588) from PL1801, Gill locality 1, Mooroolbark, Victoria. Paratype NMV P14589 (pygidium, figured Gill, 1949: pl. 9 fig. 7) from PL1801. For locality see Fig. 23.

Registered material. 57 specimens: 1 articulated dorsal exoskeleton, 1 disarticulated dorsal exoskeleton, 1 enrolled cephalothorax, 9 cephalae, 7 cranidia, 3 librigenae, 12 thoracic segments, 23 pygidia. NMV P304527 from PL1805, Gill locality 5, Coldstream, Victoria. NMV P304531, P304532 from PL1990, Coldstream. NMV P304528–P304530 from PL1813, Gill locality 13, Mooroolbark. NMV P304524–P304526 from PL1887, Gill locality 87, Mooroolbark. NMV P3204533, NMV P304570 from PL1869, Gill locality 69, Mooroolbark. NMV P304549–P304558 from PL1801. NMV P304567, P304569 from PL6661, Lilydale, Victoria. NMV P457, NMV P304559–P304562 from PL1802, Gill locality 2, Lilydale. NMV P304516–P304518 from PL1810, Gill locality 10, Lilydale. NMV P304522 from PL1858, Gill locality 58, Lilydale. NMV P304534–P304548, NMV P304566 from PL1859, Gill locality 59, Lilydale. NMV P304523 from PL1862, Gill locality 62, Lilydale. NMV P304520, P304521 from PL1829, Gill locality 29, Kilsyth, Victoria. NMV P304563–P304565 from “Lilydale”. NMV P304519 from “within 1 km of Mooroolbark Railway Station”. NMV P304571 probably from the Lilydale area. For localities see Fig. 23.

Stratigraphic distribution. Humevale Siltstone, from 1750 m above the base of the unit up to a horizon 3700 m above the base of the unit, upper *Boucotia australis* Assemblage Zone to lower *Boucotia loy-olensis* Assemblage Zone, late Lochkovian–earliest Pragian.

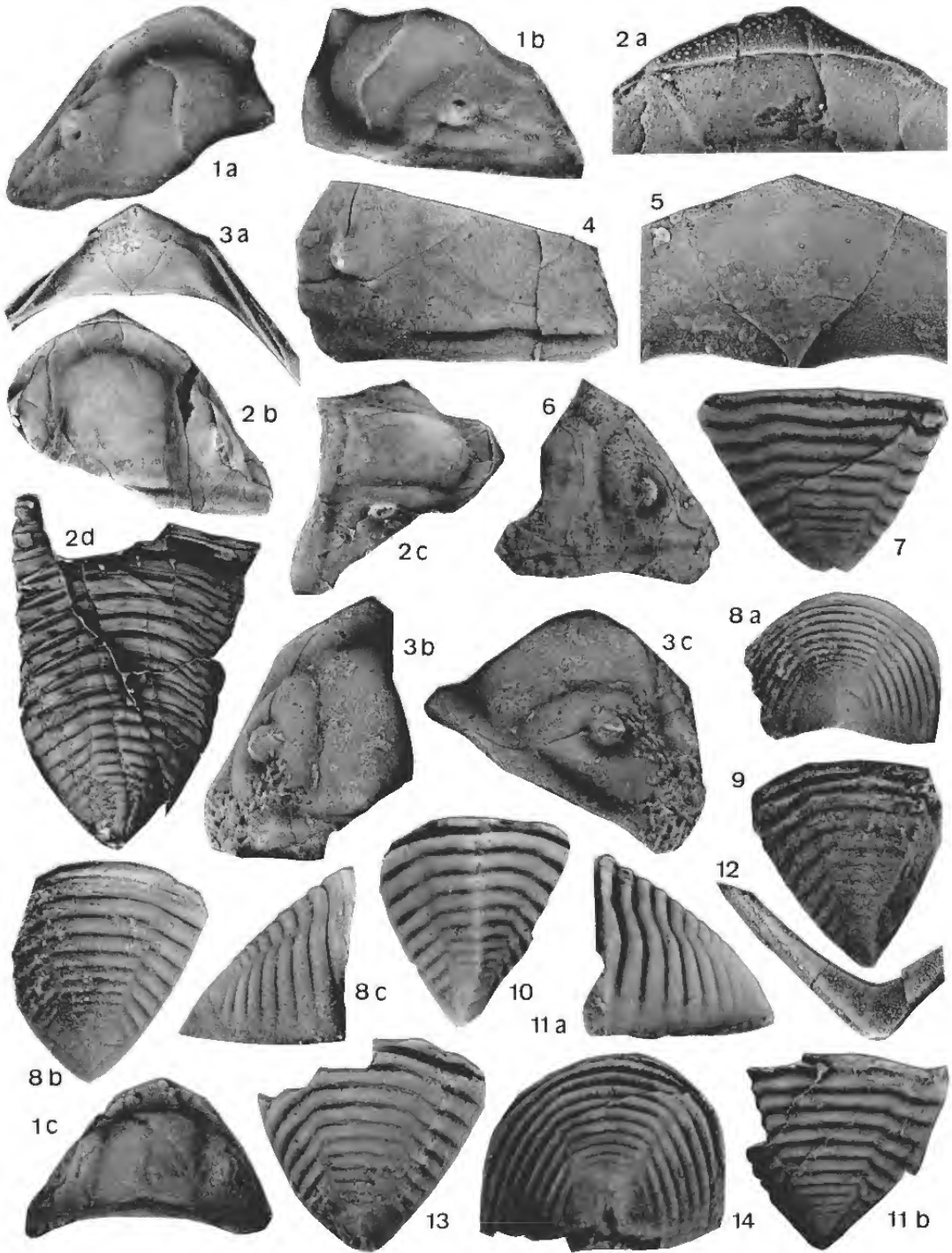
Diagnosis. Cephalon weakly pentangular in outline, with length 0.56 times width. Glabellar length equalling width, sides

straight, weakly tapering (15°), strongly rounded anteriorly. Glabellar lobation weakly defined. Palpebral lobe placed with midline opposite 0.5 cranial length. Preglabellar field (excluding rostral plate) 0.15 times cranial length. Anterior cranial margin evenly rounded, concentric with glabellar anterior margin. Dorsal surface of rostral plate crescentic in shape, length (sag.) 0.05 times cephalic length, anterior margin obtusely angular (130°). Ventral surface of rostral plate wide, kite-shaped, width 1.15 times length. Pygidium triangular, length 0.8 times width, tip obtusely pointed (~100°). Axis very wide anteriorly, width 0.66 times pygidial width, length 0.92 times pygidial length, sides straight. 9–11 axial rings, 8 pleural ribs, ring and pleural furrows deep. Surface of cephalon with fine tubercles, more distinct and densely distributed adjacent to the cephalic margin.

Description. Exoskeleton with maximum size moderate (estimated 20 cm from NMV P304562).

Cephalon with pentangular outline, sides converging forwards at 70–75° opposite glabella and at about 135° opposite preglabellar field, length about 0.57 times width. Glabella with length 0.75 times cephalic length, width 0.45 times cephalic width, sides converging at 13–17°, length ranging between 1.06–0.91 times width. Occipital ring length 0.1 times cranial length, slightly wider medially. Occipital furrow deep on internal moulds, shallow on external moulds, weak forward flexure medially. Glabellar anterior margin well defined, with arc of curvature centred at 0.55 times glabellar length. Glabella weakly convex (tr., sag.). Glabellar lobation very weakly defined (best seen on NMV P304562 and NMV P304516, Figs 24.2, 24.4), L1 0.22 times glabellar length, L2 and L3 0.11 times glabellar length. S3 transverse, S2 directed inwards-backwards at about 7° from the transverse and S1 at 15° from the transverse. Axial furrows wide, shallow posteriorly, moderately impressed anteriorly, paraglabellar areas poorly defined. Preglabellar field of uniform width, flat. Length (exsag.) of posterior border equal to occipital length abaxially, lengthening adaxially to 2.0 times occipital length. Posterior border furrow transverse, shallow and very wide, meeting lateral border furrow distally. Postocular fixigenal area short, length (exsag.) 0.14 times cranial length. Palpebral lobe 0.13 times cranial 1.75 times preoccipital glabellar width, very shallow δ - δ length, palpebral furrow. Preocular fixigena area wide, 0.22 narrowing forwards anteriorly. Anterior branches of facial suture broadly curved, meeting connective sutures almost at margin opposite 0.9 cephalic length. Librigena with wide, moderately impressed border furrow, librigenal area weakly convex, steeply inclined, lateral border wide and convex, shallow, wide subocular furrow. Dorsal surface of rostral plate slightly inclined (in lateral view, see Figs 24.2c, 24.3c), length (exsag.) 0.18 times width (tr.). Ventral surface of rostral plate kite-shaped, with slightly medial flexure (tr.) giving anterior

Figure 24. *Wenndorfia lilydalensis* (Gill, 1949). 1a, holotype NMV P14587, cephalon, dorsal view $\times 2.3$ (latex cast) from PL1801. 1b, same, oblique view $\times 2.5$. 1c, same, dorsal view $\times 1.8$ (internal mould). 2a, NMV P304516, cephalon and displaced thoracopygon, dorsal view, enlargement of anterior margin of cephalon $\times 5.0$ (latex cast) from PL1810. 2b, same, dorsal view of cephalon $\times 1.5$ (internal mould). 2c, same, oblique view of cephalon $\times 1.4$ (latex cast). 2d, same, dorsal view of thoracopygon $\times 1.3$ (latex cast). 3a, NMV P304536, cephalon, ventral view (double) $\times 2.2$ (latex cast) from PL1859. 3b, same, dorsal view $\times 2.25$. 3c, same, lateral view $\times 2.55$. 4, NMV P304562, cephalon, dorsal view $\times 2.2$ (internal mould) from PL1802. 5, NMV P304531, cephalon, ventral view (double) $\times 3.3$ (latex cast) from PL1990. 6, NMV P304528, cephalon, dorsal view $\times 1.3$ (latex cast) from PL1813. 7, NMV P304550, pygidium, dorsal view $\times 1.4$ (internal mould) from PL1801. 8a, NMV P304565, pygidium, posterior view $\times 2.9$ (latex cast) from “Lilydale”. 8b, same, dorsal view. 8c, same, lateral view. 9, NMV P304534, pygidium, dorsal view $\times 2.2$ (internal mould) from PL1859. 10, paratype NMV P14589, pygidium, dorsal view $\times 2.1$ (internal mould) from PL1801. 11a, NMV P304549, pygidium, lateral view $\times 1.6$ (internal mould) from PL1801. 11b, same, dorsal view (latex cast). 12, NMV P304566, pygidium, ventral view (double) $\times 2.8$ (internal mould) from PL1859. 13, NMV P457, pygidium, dorsal view $\times 1.5$ (internal mould) from PL1802. 14, NMV P304550, pygidium, dorsoposterior view $\times 1.7$ (internal mould) from PL1801.



margin of cephalon a very weak M-shaped outline, flat posteriorly. Connective sutures weakly sinusoidal, diverging at 90° posteriorly and at 50° anteriorly. Posteriorly, connective sutures are either confluent immediately anterior to the meeting of the hypostomal suture (NMV P304536, Fig. 24.3a), or meet the hypostomal suture separately (NMV P304531, Fig. 24.5).

Thorax with 13 segments. On external moulds axial furrows and the pleural flexure are not defined, although the axis is marked on internal moulds by exsagittal line of deep depressions (axial articulating processes) on the posterior margin of each segment. Pleural furrows wide and deep, pleural tips rounded.

Pygidium with sides weakly and uniformly convex. Axial furrows converging at about 45°, indistinct opposite first and second rings, shallow posteriorly. Axis poorly defined posteriorly without postaxial ridge. Pleural furrows not reaching margin, border poorly defined and lacking independent convexity from pleural field, without border furrow. In posterior view anterior margin strongly convex, posterior margin weakly arched to accommodate rostral flexure. In lateral view dorsal margin steep (~45°) and gently curved, ventral margin more or less horizontal.

Discussion. *Trimerus lilydalensis* exhibits several features indicative of assignment to *Wenndorfia*, including the strongly rounded anterior glabellar margin and the concentric anterior cranial margin, the antero-medial rostral node, the weak pygidial trilobation, and the termination of the pygidial axis at about 0.9 pygidial length. The species was originally described from a limited number of poorly preserved specimens, but is redescribed from a much larger population.

Gill's (1949) description of the species includes several of the diagnostic characters listed above, although the revised diagnosis differs in a number of points. Gill described the cephalon as being markedly inflated (it is only moderately convex, see Fig. 24.2c), and the exoskeleton as being smooth (it bears fine tubercles and pits, see Fig. 24.2a).

Holloway and Neil (1982) considered specimens of *Digonus wenndorfi* from the Heathcote area to be possibly conspecific with *Wenndorfia lilydalensis*. *W. lilydalensis* can be easily distinguished from *wenndorfi* in having pygidia lacking a raised postaxial ridge, and cranidia with a U-shaped rather than quadrate anterior margin, a more weakly tapered glabella with a more rounded anterior margin, and a forwardly convex rather than transverse rostral suture.

Wenndorfia lilydalensis is most closely comparable to the contemporary *W. bostoviensis* from the upper Lochkovian of Poland. The species share a similar trapezoid, moderately tapering, straight-sided glabellar outline and a very wide (tr.) palpebral area. Glabellar lobation is variably expressed in *lilydalensis*, and although Tomczykowa (1975) noted an absence of glabellar lobation for *bostoviensis*, shallow S1-S3 can be seen on specimens considered here to be conspecific with *bostoviensis* (see discussion above). More significantly, *bostoviensis* also exhibits a relatively undervied pygidium, with a triangular pygidial outline with an acutely angled tip. Pygidial axial furrows are moderately impressed on *bostoviensis*, distinguishing it from *lilydalensis* and younger species of *Wenndorfia*, that share very shallow to effaced pygidial axial furrows. The only other *Wenndorfia* to exhibit a triangular pygidial outline is the lower Pragian Polish *W. nova*, with less elongate pygidial proportions and a very narrow

pygidial axis. In cranial morphology *nova* shows some resemblance to *lilydalensis*, although the former differs in having narrow palpebral areas.

Wenndorfia lilydalensis is confined to the Lilydale sequence. One specimen labelled as coming from the Seville area, collected by F. Chapman, was found to have a counterpart labelled as coming from the Lilydale area, collected by J. Jutson. The lithology of the specimen matches lithologies from the Lilydale sequence rather than those from Seville. Gill's (1938) record of the species from PL1835, Gill locality 35, Seville is also probably erroneous, as the lithology of the specimen is unlike that at PL1835, but again closely matches lithologies of the Lilydale sequence.

Environmental notes. The faunal associations of *Wenndorfia lilydalensis* are complex. *W. lilydalensis* first appears as a rare element in the trilobite fauna (relative abundance 2%), but through its range steadily increases in relative abundance, reaching maximum relative abundance in the upper horizons of its range. In the lower part of its range *lilydalensis* frequently occurs in phacopid-dominated assemblages, but in the upper parts of its range *lilydalensis* is frequently part of a distinct acastid/homalonotid dominated association.

With the exception of a complete exoskeleton from a bioclastic coquina sandstone at PL1805 (taphofacies TIII), all specimens of *Wenndorfia lilydalensis* are found in a siltstone lithology preserved as isolated sclerites or partly disarticulated specimens including cephalon, a cephalon with 7 thoracic segments, and a moult assemblage, being a cephalon lying obliquely over the thorax. A cranidium and nearby pygidium on the same bedding plane might also be interpreted as a moult assemblage (taphofacies TIV). An outer shelf setting is suggested as the preferred environment of *W. lilydalensis*, which ranges only as a rare faunal element to mid shelf settings and to even deeper settings where it occurs with a calymenid-phacopid association. The taphonomy of the latter, with a high degree of articulation and containing sparsely distributed moult assemblages and rare enrolled specimens represents a new taphofacies for central Victoria, designated taphofacies TV, equivalent to Speyer and Brett's (1986) taphofacies 4B (see Fig. 6).

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and Mr Robert Jones at the Australian Museum for the loan of a well-preserved cranium of *Trimerus* (*Trimerus*) *harrisoni*, regrettably lost.

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Pliocene marine mammals from the Whalers Bluff Formation of Portland, Victoria, Australia

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Abstract

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The most diverse and locally abundant Australian fossil marine mammal assemblages are those from late Neogene (Late Miocene through Late Pliocene) sediments in Victoria and Flinders Island, Tasmania. However, none of these assemblages have hitherto been described. The Pliocene (>2.5–4.8 Ma) Whalers Bluff Formation, exposed in beach cliff sections and offshore reefs, at Portland, western Victoria (38°19'S, 141°38'E) has yielded a small but moderately diverse assemblage of marine mammals represented by fragmentary material. Taxa present include: right whales (Balaenidae); rorqual whales (Balaenopteridae); a physterid similar to the extant sperm whale (cf. *Physeter* sp.); the first Australian fossil record of pygmy sperm whales (Kogiidae); at least three genera of dolphins (Delphinidae: cf. *Tursiops* sp., *Delphinus* sp. or *Stenella* sp., and an undetermined genus and species); and probable earless or true seals (Phocidae). This small assemblage represents the first Australian fossil marine mammal assemblage to be described in detail. The taxonomic composition of this Pliocene marine mammal assemblage is generally similar to the present day marine mammal assemblage in north-west Bass Strait. The occurrence of extant cetacean genera in the Portland Pliocene and Flinders Island Cameron Inlet Formation assemblages indicates that the marine mammal fauna off south-east Australia had acquired an essentially modern aspect by the Late Pliocene. Several of the cetacean genera recorded in the Portland Pliocene assemblage also occur in similar-aged assemblages in other ocean basins. This corroborates the hypothesis that many cetacean taxa that are widely distributed in the world's oceans today were equally widespread during the Pliocene.

Keywords

Cetacea, Carnivora, Pinnipedia, Phocidae, Mysticeti, Odontoceti, Australia, Victoria, Portland, Whalers Bluff Formation, Pliocene

Introduction

The Pliocene epoch (1.8–5.3 Ma) is generally considered to be the time during which the modern marine mammal fauna evolved, with the extinction of archaic taxa (as well as some taxa with novel adaptations), and widespread geographic distribution of extant families and genera (Barnes, 1977; Fordyce, 1989; Fordyce and Barnes, 1994; Fordyce and Muizon, 2001; Fordyce et al., 2002; Deméré et al., 2003). Although the Pliocene marine mammals of the North Pacific (e.g. Barnes, 1973a, 1977, 1998) and eastern tropical Pacific (e.g. Muizon, 1981, 1984; Muizon and DeVries, 1985; Muizon and Domning, 1985, 2002) have been described and discussed in some detail, the Pliocene marine mammals of the Southwest Pacific (Australia and New Zealand) remain poorly known (Fordyce et al., 2002: 53). This is despite the fact that Australian late Neogene marine mammals (mostly cetaceans) are relatively abundant in museum collections,

especially the Palaeontology Collections of Museum Victoria, Melbourne.

The majority of Pliocene marine mammal fossils in these collections are rather fragmentary with one partially complete skull and associated skeleton known (NMV P179005, cf. *Megaptera* sp.). Despite this general lack of diagnostic skull material, some details of the SW Pacific Pliocene marine mammal fauna may be filled in by the study of certain isolated skeletal elements such as periotics. As noted by Barnes (1977: 322), study of these isolated elements may provide data on the taxonomic diversity within an assemblage and wider fauna. Pliocene marine mammal assemblages have hitherto not been described from Australia, so descriptions of even fragmentary material provide an initial basis for understanding marine mammal evolution off southern Australia during the Pliocene. This description of marine mammals from the Pliocene Whalers Bluff Formation assemblage comprises a preliminary basis for the late Neogene fossil record of marine mammals in Australia.

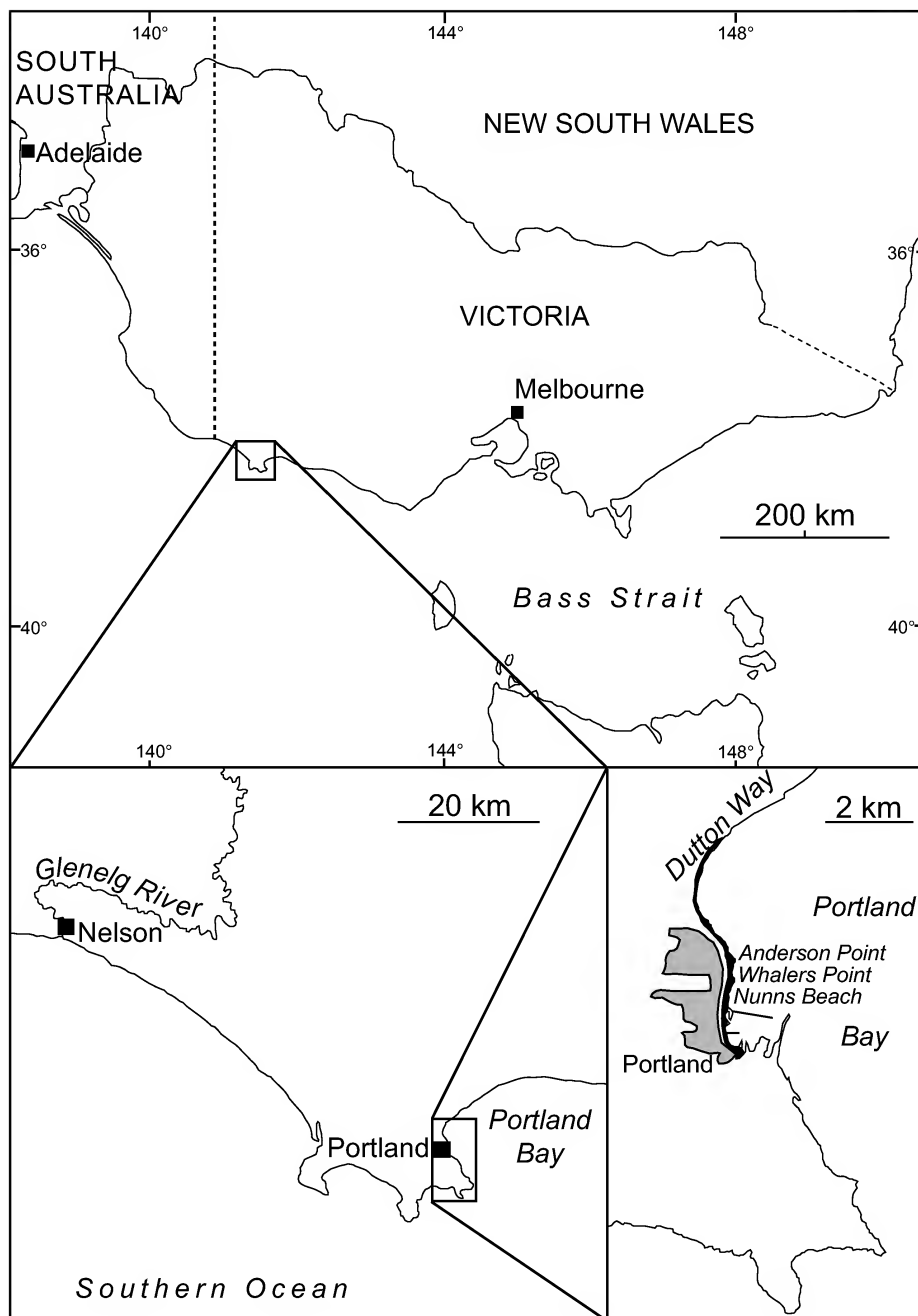


Figure 1. Locality of Portland in Victoria, south-east Australia, and the Portland fossil marine vertebrate localities. Fossils have been collected as float along the beach and from adjacent cliffs between Dutton Way and Portland Harbour. Black shading indicates areas of cliff outcrop of the Whalers Bluff Formation.

All fossils were collected from coastal exposures of the Whalers Bluff Formation lining Portland Bay in western coastal Victoria, southeast Australia (38°19'S, 141°38'E) (Fig. 1). Unfortunately, details of the geological context of virtually all fossils are unknown apart from whether the fossils were collected from the Whalers Bluff Formation or underlying limestone. Fitzgerald (2004a, 2004b) mentioned the Portland fossil marine mammals in previous publications. Bearlin (1987: 177) briefly noted the occurrence of cf. *Balaena* sp., and cf. *Balaenoptera* sp. in private collections in an unpublished Ph.D. thesis. The vertebrate faunal list for Portland given by Fitzgerald (2004b: 186) was completed prior to the recognition of two distinct, stratigraphically/temporally disjunct marine vertebrate assemblages at Portland. The majority of the vertebrates listed by Fitzgerald (2004b) were derived from the Pliocene Whalers Bluff Formation although some vertebrates from the Portland Late Miocene assemblage were listed under the Whalers Bluff Formation assemblage. The Portland Late Miocene marine vertebrate assemblage, from the Port Campbell Limestone, is considerably more diverse than the Pliocene Whalers Bluff Formation assemblage, and is to be described in a subsequent publication. Below is an emended list of the vertebrates recorded in the assemblage from the Whalers Bluff Formation at Portland.

Chondrichthyes

- Isurus* sp.
- Carcharodon carcharias* Linnaeus, 1758
- Carcharodon megalodon* Agassiz, 1835
- Myliobatis* sp.
- Ischyodus dolloi* Leriche, 1902

Mammalia

Marsupialia

- ?*Dasyuromorphia* incertae sedis
- Diprotodontidae gen. et sp. undet.
- Diprotodontidae gen. et sp. undet. C
- Diprotodontidae gen. et sp. undet. A
- Zygomaturinae gen. et sp. undet. T
- Palorchestes* sp.
- Vombatidae gen. et sp. undet.
- Sthenurus* sp.
- Protemnodon* sp.
- Macropus* sp.
- Macropodidae gen. et sp. undet. C
- Ektopodontidae gen. et sp. undet.

Rodentia

- Rodentia incertae sedis

Carnivora

- ?Phocidae gen. et sp. indet.

Cetacea

- Balaenidae gen. et sp. indet.
- Balaenopteridae gen. et sp. indet.
- cf. *Physeter* sp.
- Kogiidae gen. et sp. indet.
- Delphinioidea incertae sedis
- cf. *Tursiops* sp.
- Delphinus* sp. or *Stenella* sp.
- Delphinidae gen. et sp. undet. A

Materials and methods

All fossil specimens were collected by Mr Sean Wright of Portland and are in the Palaeontology Collections of Museum Victoria. Anatomical terminology for periotics and tympanics follows Evans (1993), Fordyce (1994), Fordyce and others (2002) and Kasuya (1973) with minor modifications. All periotic and tympanic measurements follow the methods and dimensions outlined by Kasuya (1973) and were made using vernier callipers. Photographs were taken using a 35 mm Nikon Nikkormat EL SLR with a 105 mm macro-lens, and a Nikon D70 digital SLR with a 60 mm macro-lens. Where indicated, specimens were coated with a sublimate of ammonium chloride to enhance contrast in black and white (denoted by AC in figure captions). Where necessary, fragile specimens were consolidated with a hardener consisting of 3% solution of Paraloid B72 (ethyl methacrylate/methyl acrylate copolymer) in acetone.

Institutional abbreviations. NMV C, Museum Victoria Comparative Anatomy Collection, Melbourne; NMV P, Museum Victoria Palaeontology Collection, Melbourne; CD, Phylum Chordata catalogue, New Zealand Geological Survey, Lower Hutt; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, DC. For a complete list of specimens referred to in this study, see table 1.

Geology and age of the Whalers Bluff Formation

For about 4 km along cliffs north of Portland Harbour the Pliocene Whalers Bluff Formation is exposed (Singleton et al., 1976). This formation is about 7.6 m thick, being comprised of horizontally bedded fossiliferous clay, oyster-rich beds and sandy limestones (Abele et al., 1988). These sediments unconformably overlie the Upper Miocene Port Campbell Limestone and infill a karst topography developed in the top of the Miocene limestone (Boutakoff and Sprigg, 1953; Dickinson et al., 2002). The Whalers Bluff Formation is unconformably capped by basalts.

The age of the Whalers Bluff Formation is well constrained relative to some other Neogene marine mammal-bearing units in the SW Pacific (Fig. 2). However, the determination of the younger age limit of the Whalers Bluff Formation has proved problematic. The Port Campbell Limestone which underlies the Whalers Bluff Formation is Late Miocene (indicated by presence of *Globorotalia miotumida*; planktonic foraminiferal zones N16-basal N17; Tortonian; 8–10.8 Ma) (Dickinson et al., 2002). Deposition of the Whalers Bluff Formation began during planktonic foraminiferal zone N19 (indicated by the presence of *Globorotalia puncticulata* at the base of the formation) and ensued into the base of planktonic foraminiferal zone N21 (Fig. 2) (Singleton et al., 1976; Dickinson et al., 2002). K-Ar dates of 2.51 Ma from basalts that cap the Whalers Bluff Formation have been reported (Singleton et al., 1976).

Beu and Darragh (2001) have suggested that the Whalers Bluff Formation is latest Pliocene to earliest Pleistocene (>1.5–2.0 Ma) based on the presence of the pectinid bivalve *Pecten fumatus* Reeve, 1852 in a section along the Glenelg River. However, *Pecten fumatus* does not occur in the Whalers Bluff Formation at Portland (Darragh in Singleton et al., 1976; T.A. Darragh, pers. comm.). *Zenatiopsis ultima* Darragh and Kendrick, 1971 occurs in the Whalers Bluff Formation at Portland but is a Pliocene species and never occurs with

Table 1. Specimens referred to in this study. For more detailed locality/stratigraphic data see Fitzgerald (2004b). Abbreviations: e=Early; m=Middle; l=Late; M=Miocene; P=Pliocene; Pt=Pleistocene; R=Recent; Vic. = Victoria; Tas. = Tasmania; NZ = New Zealand.

Specimen	Taxon	Locality	Formation	Age
NMV P221242	<i>Isurus</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P218415	<i>Carcharodon megalodon</i>	Portland, Vic.	Whalers Bluff	P
NMV P218418	<i>Carcharodon carcharias</i>	Portland, Vic.	Whalers Bluff	P
NMV P218470	<i>Myliobatis</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P218296	<i>Ischyodus dolloi</i>	Portland, Vic.	Whalers Bluff	P
NMV P221241	?Dasyuromorphia gen. et sp. undet.	Portland, Vic.	Whalers Bluff	P
NMV P218500	Diprotodontoidea gen. et sp. undet.	Portland, Vic.	Whalers Bluff	P
NMV P218498	Diprotodontoidea gen. et sp. undet. C	Portland, Vic.	Whalers Bluff	P
NMV P218499	Diprotodontidae gen. et sp. undet. A	Portland, Vic.	Whalers Bluff	P
NMV P221230	Zygomaturinae gen. et sp. undet. T	Portland, Vic.	Whalers Bluff	P
NMV P221231	<i>Palorchestes</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P221238	Vombatidae gen. et sp. undet.	Portland, Vic.	Whalers Bluff	P
NMV P221232	<i>Protemnodon</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P221235	<i>Macropus</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P221227	? <i>Macropus</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P221237	<i>Sthenurus</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P221229	Macropodidae gen. et sp. undet. C	Portland, Vic.	Whalers Bluff	P
NMV P197795	Ektopodontidae gen. et sp. undet.	Portland, Vic.	Whalers Bluff	P
NMV P221240	Rodentia indet.	Portland, Vic.	Whalers Bluff	P
NMV P218273	?Phocidae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218465	?Phocidae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218269	Balaenidae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218268	Balaenopteridae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218298	cf. <i>Physeter</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P218407	Kogiidae gen. et sp. indet.	Portland, Vic.	Whalers Bluff	P
NMV P218283	Delphinoidea incertae sedis	Portland, Vic.	Whalers Bluff	P
NMV P218284	Delphinoidea incertae sedis	Portland, Vic.	Whalers Bluff	P
NMV P218286	Delphinoidea incertae sedis	Portland, Vic.	Whalers Bluff	P
NMV P218266	cf. <i>Tursiops</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P218265	<i>Delphinus</i> or <i>Stenella</i> sp.	Portland, Vic.	Whalers Bluff	P
NMV P218264	Delphinidae gen. et sp. undet. A	Portland, Vic.	Whalers Bluff	P
NMV P16198	?Phocidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P41759	Phocidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P42523	?Phocidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P160399	Phocidae gen. et sp. undet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P160433	Phocidae gen. et sp. undet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P160441	Phocidae gen. et sp. undet.	Grange Burn, Vic.	Grange Burn	eP
NMV P215759	?Phocidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P16195	Balaenidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	eP
NMV P48865	Balaenidae gen. et sp. indet.	Grange Burn, Vic.	Grange Burn	eP
NMV P160438	Balaenidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P197824	Balaenidae gen. et sp. indet.	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P171503	<i>Balaenoptera edeni</i> or <i>B. brydei</i>	Tidal River, Vic.	N/A	R
NMV P179005	<i>Megaptera</i> sp.	Lakes Entrance, Vic.	Jemmys Point	eP
NMV P23961	? <i>Mesoplodon</i> sp.	Cameron Inlet, Tas.	Cameron Inlet	P
NMV P13033	" <i>Steno</i> " <i>cudmorei</i>	Beaumaris, Vic.	Black Rock Sandstone	lM-eP
NMV P204352	Delphinidae gen. et sp. undet. A	Henley, England	Red Crag	P-Pt
NMV P218481	Delphinidae gen. et sp. undet. A	Henley, England	Red Crag	P-Pt
NMV C24972	<i>Kogia breviceps</i>	Cape Conran, Vic.	N/A	R
NMV C24976	<i>Kogia breviceps</i>	Shelley Beach, Vic.	N/A	R
NMV C27879	<i>Eubalaena australis</i>	Altona Bay, Vic.	N/A	R
NMV C28892	<i>Megaptera novaeangliae</i>	Venus Bay, Vic.	N/A	R
CD 53	Delphinidae gen. et sp. undet. A	Chatham Island, NZ	Unnamed	?P
USNM 22953	<i>Orycterocetus crocodilinus</i>	Calvert County, USA	Calvert	mM
USNM 183007	Physeteridae gen. et sp. undet.	Lee Creek Mine, USA	Yorktown	eP
USNM 452993	<i>Scaphokogia cochlearis</i>	Aguada de Lomas, Peru	Pisco	lM
USNM 183008	Kogiidae gen. et sp. undet.	Lee Creek Mine, USA	Yorktown	eP
USNM 251118	Kogiidae gen. et sp. undet.	Lee Creek Mine, USA	Yorktown	eP

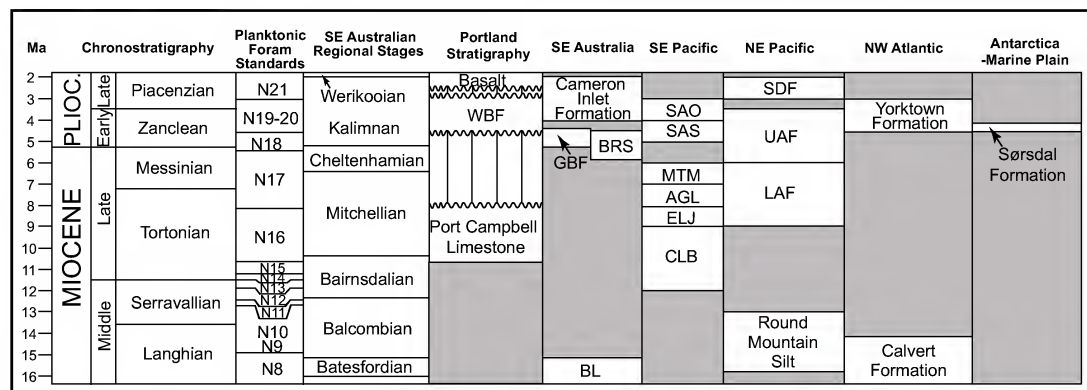


Figure 2. Stratigraphic correlation of the Portland fossil marine mammal-bearing formations with selected major late Neogene marine mammal-bearing units. Stratigraphy and geochronology are from Barnes (1973, 1977, 1984, 1998), Muizon and DeVries (1985), Muizon and Bellon (1986), Gottfried et al. (1994), Whitmore (1994), Prothero (1998), Fordyce (2002a), Fordyce et al. (2002), Fitzgerald (2004b), Muizon et al. (2004), Barnes et al. (2005) and Gradstein et al. (2004). Abbreviations: **AGL**, Pisco Formation, Aguada de Lomas level; **BL**, Batesford Limestone; **BRS**, Black Rock Sandstone; **CLB**, Pisco Formation, Cerro la Bruja; **ELJ**, Pisco Formation, El Jahuay level; **GBF**, Grange Burn Formation; **LAF**, Lower Member, Almejas Formation; **MTM**, Pisco Formation, Montemar level; **SAO**, Pisco Formation, Sacaco level; **SAS**, Pisco Formation, Sud-Sacaco level; **SDF**, San Diego Formation; **UAF**, Upper Member, Almejas Formation; **WBF**, Whalers Bluff Formation.

P. fumatus, the latter first appearing at the base of the Pleistocene (T.A. Darragh, pers. comm.).

These data indicate that the Whalers Bluff Formation at Portland is Early to Late Pliocene (Zanclean to Piacenzian; >2.5–4.8 Ma). Further study of terrestrial mammals from the Whalers Bluff Formation may help refine the geological age of this unit. Unfortunately, the exact bed from which fossil vertebrates were collected within the Whalers Bluff Formation is unknown. Thus, a finer age resolution than that given above for the assemblage is currently unavailable. The age range of the Whalers Bluff Formation presented herein is considered to be the best estimate based on available data and the reader must be cautioned that future work may yield a younger limit on the minimum age.

The Whalers Bluff Formation (as well as, in part, laterally equivalent Victorian marine mammal-bearing units such as the Grange Burn Formation, Black Rock Sandstone and Jemmys Point Formation) has been interpreted as representing a prograding quartz-carbonate barrier system with the clastic-dominated units listed above representing an initial marine incursion (Dickinson et al., 2002: 290).

Systematics of marine mammals

Order **Cetacea** Brisson, 1762

Suborder **Mysticeti** Flower, 1864

Family **Balaenidae** Gray, 1821

Genus and species indeterminate

Referred specimen. NMV P218269, incomplete right periotic; anterior and superior processes virtually complete, but pars cochlearis almost entirely worn off, and only anteriormost base of posterior process preserved (Fig. 3A).

Description. P218269 is highly polished and abraded. The anterior process is blunt and globose, being indistinct from the superior process. There is marked lateral exostosis of the superior process lateral to the epitympanic recess. The lateral aspect of the anterior process is rugose and pitted. Posteriorly, this pitting decreases in density. Only the lateralmost region of the pars cochlearis is preserved. In medial view, the most notable feature is the sulcus for the facial nerve (cr. VII), the course of cr. VII being preserved from its entry into the body of the periotic at the aperture of the internal facial foramen, to its ventral exit into the epitympanic cavity via the ventral facial foramen. All other features of the pars cochlearis and epitympanic recess have been obliterated. Posterior to the broad and shallow hiatus epitympanicus is a remnant of the base of the posterior process (which is directed posterolaterally and somewhat ventrally).

Discussion. Miller (1924: 8–9) listed the following features that distinguish the periotics of Balaenidae from those of Balaenopteridae (and other baleen-bearing Mysticeti): (1) axis of anterior process of periotic parallel with axis of internal acoustic meatus; (2) [longitudinal] axes of anterior and posterior processes converge at an acute angle; and (3) pars cochlearis small relative to rest of periotic. In addition to the preceding features, the possession of massive lateral exostosis of the anterior process and anterolateral superior process, such that the anterior process appears swollen (as noted by Fordyce, 1982: 48), seems to be a feature shared by all extant and late Neogene balaenid periotics. It is largely on the basis of the latter character and the phenetic similarity of P218269 to a periotic (P16195) from the Lower Pliocene Black Rock Sandstone of Beaumaris identified as belonging to cf. “*Balaena*” (Gill, 1957) that P218269 is referred to Balaenidae, genus and species indeterminate.

The fossil record of Balaenidae begins in the Late Oligocene (c. 28 Ma: Fordyce, 2002b), although the record only becomes reasonably well known from the Mio-Pliocene boundary onwards (McLeod et al., 1993; Bisconti, 2003). *Morenocetus parvus* Cabrera, 1926 is the geologically oldest named balaenid, from the early Early Miocene (Aquitainian) of Patagonia. From the end Aquitainian to early Tortonian of the Miocene the evolutionary history of Balaenidae is virtually unknown. The extant balaenids include *Balaena mysticetus* Linnaeus, 1758, *Eubalaena australis* Desmoulins, 1822, *E. glacialis* Müller, 1776, and *E. japonica* Lacépède, 1818 (e.g., Cummings, 1985; Reeves and Leatherwood, 1985; Bannister, 2002). Note that Rice (1998) included all extant balaenids in the genus *Balaena* and recognised only two species, *B. mysticetus* and *B. glacialis*. The taxonomic scheme of Bannister (2002) is used herein. *Balaena* is known from the Early Pliocene of the North Atlantic (McLeod et al., 1993; Westgate and Whitmore, 2002). There are very few confirmed pre-Quaternary fossil records of *Eubalaena*. Bisconti (2003, 2005) referred the Pliocene *Balaena belgica* Abel, 1941 to *Eubalaena belgica*. McLeod and others (1993: 63) suggested that a balaenid periotic from the Early Pliocene of South Australia (originally recorded by Howchin: 1919) could represent *Eubalaena* (as opposed to its original referral to *Balaena*). Dixon (1990) described an incomplete Recent *Eubalaena australis* skeleton from Altona Bay, near Melbourne, Victoria. The latter specimen (C27879) includes tympanics and periotics. The extinct genera *Balaenula* and *Balaenotus* have been recorded from the Late Miocene through Pliocene of the N Pacific (Barnes, 1977; McLeod et al., 1993) and N Atlantic (McLeod et al., 1993; Bisconti, 2003 and references therein). Recently, Bisconti (2005) described a new genus and species of relatively small balaenid, *Balaenella brachyrhynchus*, from the Early Pliocene of Belgium.

The incompleteness of P218269 and lack of information on the extent of intraspecific and ontogenetic variation in balaenid periotics, hampers comparisons with described extant and fossil balaenid taxa. Furthermore, there are as yet no published criteria for discriminating between the periotics of *Balaena* and *Eubalaena*. Despite these problems, it may be noted that P218269 is similar in overall size to several isolated balaenid periotics from the uppermost Miocene to Lower Pliocene Black Rock Sandstone and Grange Burn Formation of Victoria (e.g. P16195, P48865, P160438, and P197824). The discovery of a more complete periotic (including the pars cochlearis) is necessary before any further comparisons between the Portland Pliocene balaenid and the other Victorian specimens listed above can be made.

Family Balaenopteridae Gray, 1864

Genus and species indeterminate

Referred specimen. NMV P218268, incomplete right periotic; lacking medial three-quarters of pars cochlearis and posterior process (Fig. 3B).

Description. P218268 is polished, rolled and may be secondarily phosphatised. The anterior process is elongated and some-

what attenuated anteriorly. The dorsal surface of the anterior process is smooth, with only slight rugosity, as seen in the periotics of extant Balaenopteridae. An oblique groove on the dorsolateral surface of the anterior process near its preserved apex is interpreted as a trace of a vascular sulcus. The latter feature has previously been considered a sulcus for the capsuloparietal emissary vein (Geisler and Luo, 1998; Geisler and Sanders, 2003) or as a sulcus marking the path of an artery, specifically part of the middle meningeal artery (Fordyce, 1994). Fordyce (1994) and Watson and Fordyce (1994) described this feature as the anteroexternal sulcus whereas Geisler and Sanders (2003) treated the anteroexternal sulcus and sulcus for the capsuloparietal emissary vein as separate features. Further work is required to better establish the venous/arterial correlate of this osteological feature which in this study is referred to as the sulcus for the capsuloparietal emissary vein. In extant balaenopterids, this sulcus usually courses posteriorly to a point level with the position of the mallear fossa. However, in P218268 any more posterior continuation of the sulcus for the capsuloparietal emissary vein, if formerly present, no longer occurs due to abrasion.

The ventral presentation of the periotic exhibits several features. As occurs in extant *Balaenoptera* and *Megaptera*, the lateralmost eminence of the ventrolateral ridge of the superior process (sensu Geisler and Luo, 1996) is situated at the same level as the anterior margin of the pars cochlearis. The mallear fossa is poorly differentiated from the rest of the epitympanic recess.

The preserved posterolateral margin of the periotic is formed by the hiatus epitympanicus. The course of the facial nerve on the ventral surface of the periotic is marked by the facial sulcus which is bounded anteriorly by the aperture of the ventral facial foramen. In ventral view, a distinct bridge of bone at the anterolateral corner of the preserved pars cochlearis represents the ventral roof of the ventral facial foramen. The endocranial aspect of the pars cochlearis preserves the aperture of the internal facial foramen. Anterior to this aperture is a deep excavation in the medial surface of the periotic at the base of the anterior process. This region (composed of cancellous bone in extant balaenopterids) marks the site of ankylosis between the anterior process and the body of the periotic. As in other Balaenopteridae, the pars cochlearis appears to have been elongated towards the cranial cavity.

Discussion. That P218268 is a balaenopterid periotic is evident by the possession of: (1) elongated, triangular and anteriorly attenuated anterior process; (2) a triangular lateral eminence of the ventrolateral ridge; and (3) a relatively large pars cochlearis elongated towards the cranial cavity. Because P218268 is represented only by an incomplete periotic, it is not possible for it to be identified below family level. The size of P218268 is comparable to that of periotics of subadult *Balaenoptera edeni* Anderson, 1879 or *B. brydei* Olsen, 1913 (P171503) and juvenile *Megaptera novaeangliae* Borowski, 1781 (C28892). However, the periotics of extant *Megaptera novaeangliae* and an undescribed species of *Megaptera* from the Early Pliocene of Victoria (P179005) possess the following features which differentiate them from P218268: (1) the anterior process is

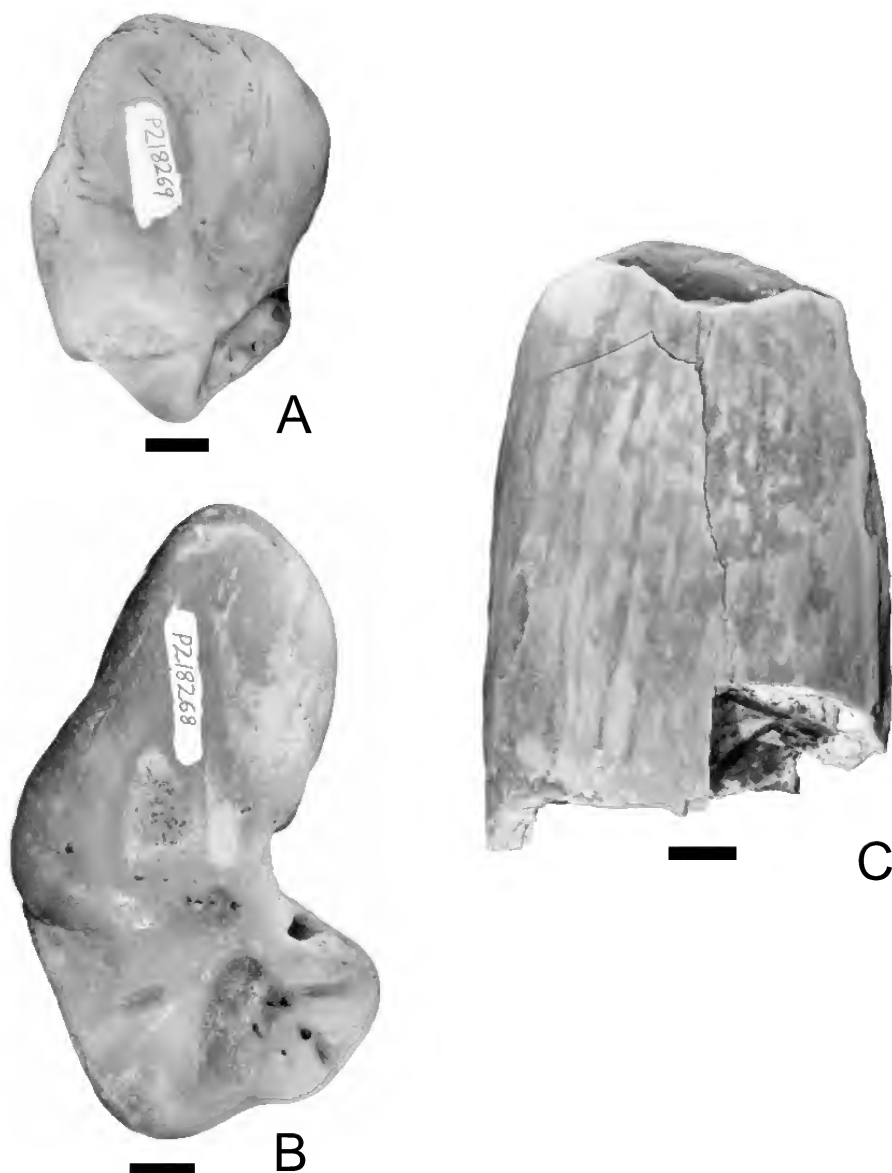


Figure 3. Mysticeti and Physteridae from the Pliocene Whalers Bluff Formation, Portland. **A**, Balaenidae gen. et sp. indet., incomplete right periotic, NMV P218269, in ventrolateral view (AC); **B**, Balaenopteridae gen. et sp. indet., incomplete right periotic, NMV P218268, in ventral view (AC); **C**, cf. *Physeter* sp., apical crown of tooth, NMV P218298, in side view (AC). Scale bars equal 10 mm.

relatively shorter; (2) anterior process is more dorsoventrally compressed; (3) in endocranial view, there is an anteroposteriorly thickened region of cancellous bone in the pars cochlearis anterior to the internal facial foramen; and (4) no deep excavation in the endocranial surface of the periotic anterior to the pars cochlearis. Many of these features may be related to ontogenetic variation. At least, the lack of these four features in P218268 may indicate that this periotic is not referable to *Megaptera* and may belong to an indeterminate species in the genus *Balaenoptera*.

Suborder **Odontoceti** Flower, 1867

Family **Physeteridae** Gray, 1821

cf. *Physeter* sp. Linnaeus, 1758

Referred specimen. NMV P218298, isolated, worn-down apical region of tooth crown (Fig. 3C).

Description. P218298 has an ovoid cross-section at its base which becomes more ellipsoid towards the preserved apex of the crown. In occlusal view, the apex of the tooth crown is incised by a deep anteroposterior cleft which is attributed to tooth wear. Shallow longitudinal grooves in the surface occur on all faces of the crown. The basal end of the tooth is broken to reveal a cross-section through the crown. The only notable feature of this aspect of the tooth is the presence of thick layers of cementum.

Discussion. The large size of this tooth and the thick layers of cementum suggest that P218298 represents a physeterid. Little more can be said about the systematics of this specimen although its size and similarity to teeth of large adult *Physeter macrocephalus* suggest affinities with the extant sperm whale.

Family **Kogiidae** Gill, 1871

Genus and species indeterminate

Referred specimen. NMV P218407, incomplete left tympanic bulla (Fig. 4A-B).

Description. The most striking aspect of the morphology of P218407 is its small size. The tympanic is polished with rolled edges being rounded off. The preserved portion includes only the medial half of the bulla with very little of the outer lip present. The base of the posterior process of the tympanic has been worn off. In dorsal and ventral view, there is a distinct furrow in the medial edge of the involucrum between the inner posterior prominence and the inner anterior prominence. In ventral view, the furrow between the prominences of the involucrum forms an obtuse angle. There is no preserved ventral keel and the median furrow is very shallow such that it is poorly differentiated from the surrounding ventral surface of the tympanic. The interprominential notch is relatively broad. The anterior edge of the involucrum and outer lip is squared-off. In dorsal view, the involucrum has a consistent width along its length, but is expanded at the level of the inner posterior prominence.

Discussion. P218407 is referred to the Kogiidae on the basis of the following features shared with extant and fossil kogiids: (1) small overall size [as Kasuya (1973: 25) noted among extant Odontoceti only *Pontoporia blainvillei* Gervais and d'Orbigny, 1844 has a smaller tympanic, and P218407 does not resemble the tympanic of that taxon]; (2) distinct embayment in the medial edge of the involucrum between the inner anterior and posterior prominences; and (3) squared-off anterior edge of the involucrum and outer lip. It should be noted that the second feature is also seen in the tympanic bullae of *Physeter macrocephalus* Linnaeus, 1758, *Orycterocetus crocodilinus* Cope, 1868 (USNM 22953) (Kellogg, 1965) (Fig. 5C-D), and an Early Pliocene physeterid (USNM 183007) (Fig. 5A, B). Despite this similarity between P218407 and the tympanics of Physeteridae, the relatively large size of physeterid tympanics precludes P218407 from being considered as a physeterid. Furthermore, the inner posterior prominence in physeterid tympanics is generally more pointed in outline than the rounded outer posterior prominences in kogiid tympanics.

Among fossil Kogiidae, the tympanics of *Praekogia cedrosensis* (Barnes, 1973b) have not been described. A skull of *Scaphokogia cochlearis* Muizon, 1988 (USNM 452993) includes an associated incomplete left tympanic (Fig. 4E, F). The tympanic of *S. cochlearis* is similar to the tympanics of extant *Kogia* in its relatively small size and possession of a distinct embayment in the medial side of the involucrum between the inner anterior and posterior prominences. The most notable difference between the tympanic of *S. cochlearis* and the Portland kogiid tympanic lies in the more marked inflation of the inner posterior prominence of P218407. *S. cochlearis* possesses a less expanded inner posterior prominence, such that the embayment in the medial face of the involucrum is not as deep as in P218407. In this respect, *Scaphokogia cochlearis* is similar to two undescribed Early Pliocene kogiids from the Lee Creek Mine, North Carolina (USNM 183008, Fig. 4G-H; USNM 251118, Fig. 4C, D) and the extant *Kogia breviceps* Blainville, 1838 (Fig. 4I, J).

The features which Kasuya (1973) used to differentiate between Recent *Kogia breviceps* and *K. sima* Owen, 1866 are not preserved in P218407. However, comparison between figures of the tympanic of *K. sima* (Kasuya, 1973: plate VIII), and actual specimens of *K. breviceps* (C24972, C24976), indicate that P218407 differs from both extant *Kogia* species in: (1) embayment in medial edge of involucrum between the inner prominences is markedly deeper; and (2) the involucrum is less dorsoventrally and mediolaterally inflated. Despite these differences, P218407 is almost identical in size to the tympanics of *Kogia breviceps*. Given that the currently available evidence is meagre, P218407 is not identified below family level. Table 2 compares some dimensions of the tympanics of kogiids and physeterids discussed above.

P218407 is the first fossil record of Kogiidae from Australia. Fossil kogiids have previously been reported in the SW Pacific region, from the ?Late Miocene of the Chatham Rise, east of New Zealand (Fordyce, 1984a) but that record has a poorly constrained age (Fordyce, 1989, 1991b).

Table 2. Measurements of tympanics of Physeteridae and Kogiidae. Measurements follow methodology of Kasuya (1973). All measurements are in mm.

	NMV C24972	NMV P218407	USNM 22953	USNM 183007	USNM 452993	USNM 183008	USNM 251118
Standard length of tympanic bulla, distance from anterior tip to posterior end of outer posterior prominence	26.0	–	31.0	42	–	29.0	31
Distance from anterior tip to posterior end of inner posterior prominence	19.9	21.6	27.0	38	28	31.0	28
Distance from posteroventral tip of outer posterior prominence to tip of sigmoid process	21.28	–	–	–	–	–	–
Distance from posteroventral tip of outer posterior prominence to tip of conical process	15.3	–	–	–	–	–	–
Width of tympanic bulla at the level of the sigmoid process	26.0	–	–	–	–	–	–
Height of tympanic bulla, from tip of sigmoid process to ventral keel	26.5	–	–	–	–	–	–
Width across inner and outer posterior prominences	19.0	–	20.2	24	–	22.5	20+

Superfamily Delphinoidea Gray, 1821

Incertae sedis

Referred specimens. NMV P218283, P218284 and P218286, all isolated teeth (not figured).

Description. P218283, P218284 and P218286 all represent small odontocete teeth possessing conical enamel-covered crowns that bear fine wrinkling ornamentation, and curve linguallly towards the crown apex. As in kentriodontids, there is a lingual bulge at the base of the crown but this feature is not as prominent in the teeth from Portland. None possesses an open pulp cavity suggesting that all were derived from adult individuals.

P218283 is an incomplete tooth, its preserved maximum length and maximum width of the crown being 16 mm and 6 mm respectively. Due to the incomplete nature of this tooth it does not warrant further description.

P218284 is the most highly polished and the most complete. It differs from the others in having a mediolaterally compressed root with a more prominent mesial-distal bulge at its midpoint. The preserved apex of the root curves posteriorly.

The most notable feature of P218286 distinguishing it from the other teeth is its bulbous root, which contrasts with the transversely flattened morphology of P218284.

Discussion. Only one delphinoid odontocete has previously been described from the Tertiary of Australia, the latest Miocene-earliest Pliocene “*Steno*” *cudmorei* Chapman (1917) from the Black Rock Sandstone of Beaumaris, Victoria (Fitzgerald, 2004b). Fordyce (1982) questioned the taxonomic identity of “*S.*” *cudmorei* (the holotype, P13033, being an isolated tooth) and Fitzgerald (2004b) referred “*S.*” *cudmorei* to Delphinidae, genus and species indeterminate. Chapman (1917) assigned P13033 to *Steno* on the basis of the resemblance of its crown ornamentation to that seen in the teeth of the extant *Steno bredanensis* Cuvier in Lesson, 1828 (e.g., Miyazaki and Perrin, 1994). Given that *Steno* is probably in a basal position in the phylogeny of Delphinidae (Miyazaki and

Perrin, 1994; LeDuc et al., 1999) and that some of the presumed ancestors of Delphinidae, the Kentriodontidae (Barnes, 1978, 2002; LeDuc, 2002), possessed *Steno*-like crown ornamentation (e.g., Kellogg, 1966), the anastomosing striae on the crown of P13033 (and P218283, P218284, P218286) are of dubious use in assessing the phylogenetic affinities of isolated teeth. Furthermore, non-delphinid small odontocetes such as *Lipotes vexillifer* Miller, 1918 possess anastomosing wrinkling on tooth crown enamel (Miller, 1918; Brownell and Herald, 1972; Barnes, 1985) which casts doubt on any perceived taxonomic or phylogenetic signal present in these teeth.

The isolated teeth from Portland are assigned to Delphinoidea incertae sedis. None of the Portland Pliocene teeth share demonstrably close affinities with the holotype tooth of “*Steno*” *cudmorei*.

Family Delphinidae Gray, 1821

cf. *Tursiops* sp. Gervais, 1855 sp.

Referred specimen. NMV P218266, virtually complete right periotic (Fig. 6).

Description. P218266 is typically delphinid in possessing: (1) posterior process of the periotic projects laterally and posterolaterally; (2) longitudinal grooves on the articular facet of the posterior process of the tympanic (this feature also occurs in Monodontidae); (3) relatively low crista transversa; (4) internal facial foramen opens at the same level as the tractus spiralis foraminosus in the internal acoustic meatus; (5) a short, blunt, rectangular anterior process of the periotic which in anterior, dorsal and ventral views appears laterally compressed; (6) a large fovea epitubaria for the accessory ossicle eliminates the anterior bullar facet on the anterior process; (7) prominent parabullary ridge; (8) inflated pars cochlearis; and (9) relatively shallow internal acoustic meatus (Kasuya, 1973; Fordyce et al., 2002). The first character is usually only seen in Delphinidae but several taxa in the extinct delphinoid grade-

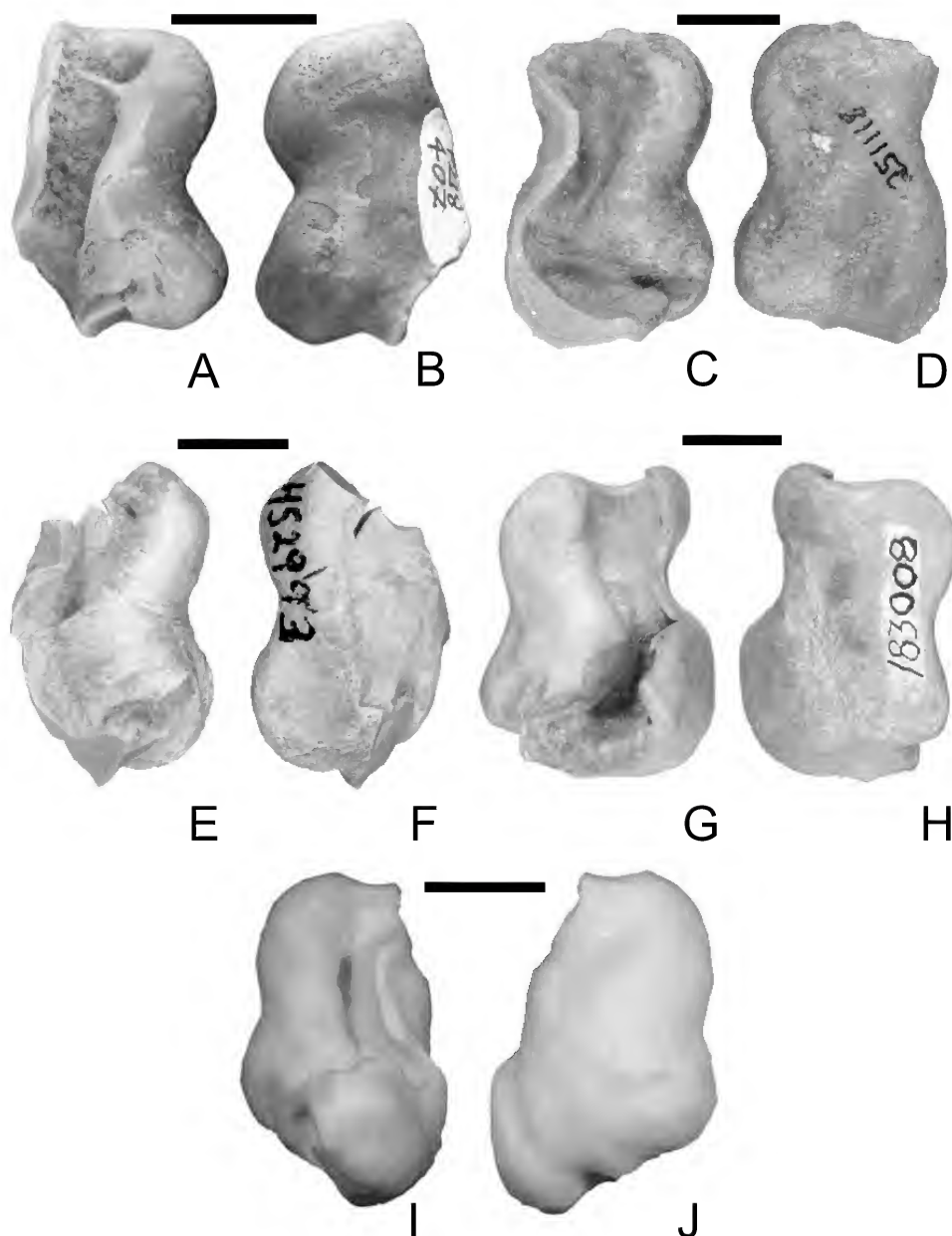


Figure 4. Miocene to Recent Kogiidae tympanics. **A-B**, Kogiidae gen. et sp. indet. (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), incomplete left tympanic, NMV P218407 (**AC**). **C-D**, Kogiidae gen. et sp. undet. (Lower Pliocene Yorktown Formation, Lee Creek Mine, North Carolina, U.S.A.), incomplete left tympanic, USNM 251118. **E-F**, *Scaphokogia cochlearis* (Upper Miocene Pisco Formation, Aguada de Lomas level, Arequipa Department, Peru), incomplete left tympanic, USNM 452993. **G-H**, Kogiidae gen. et sp. undet. (Lower Pliocene Yorktown Formation, Lee Creek Mine, North Carolina, U.S.A.), incomplete right tympanic, USNM 183008. **I-J**, *Kogia breviceps* (Recent, Shelley Beach, Victoria, Australia), incomplete left tympanic, NMV C24976. **A, C, E, G, I**, all in dorsal view. **B, D, F, H, J**, all in ventral view. Scale bars equal 10 mm.

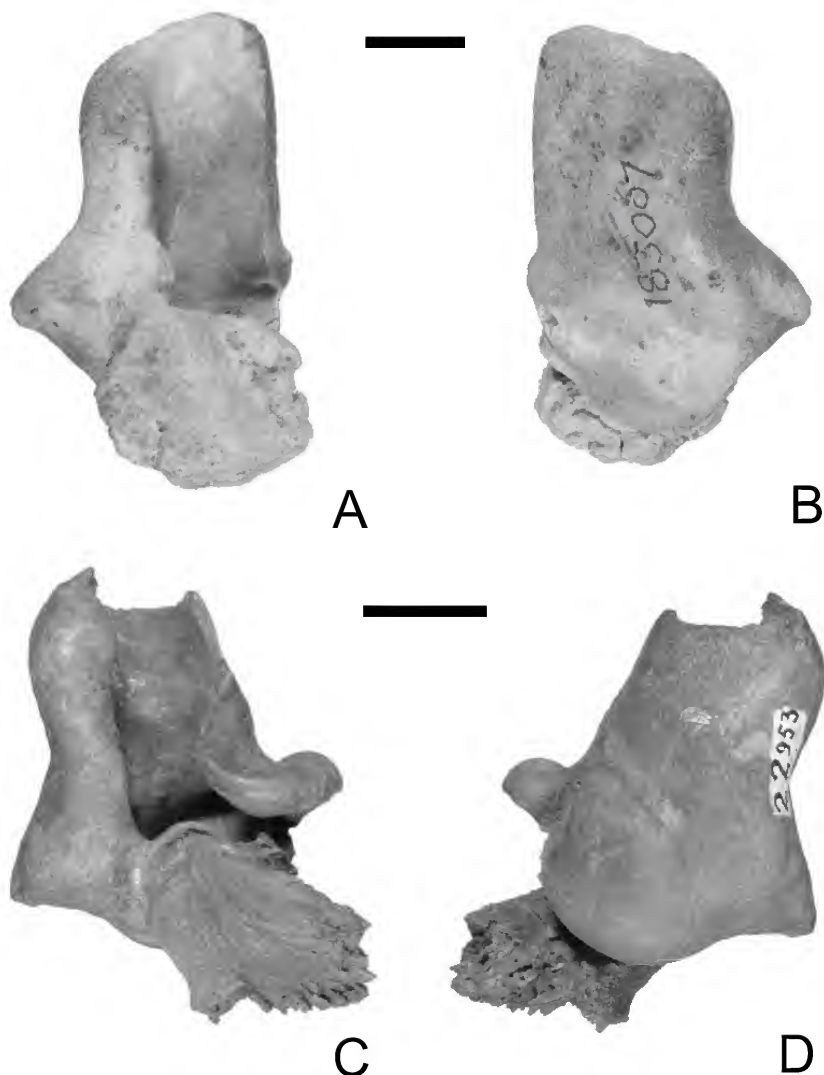


Figure 5. Miocene to Pliocene Physeteridae tympanics. **A-B**, Physeteridae gen. et sp. undet. (Lower Pliocene Yorktown Formation, Lee Creek Mine, North Carolina, U.S.A.), right tympanic, USNM 183007. **C-D**, *Orycterocetus crocodilinus* (Middle Miocene Calvert Formation, Zone 14, south of Randle Cliff Beach, Calvert County, Maryland, U.S.A.), right tympanic, USNM 22953. **A** and **C** in dorsal view. **B** and **D** in ventral view. Scale bars equal 10 mm.

taxon Kentriodontidae possess a posterolaterally projecting posterior process of the periotic (eg., Barnes and Mitchell, 1984; Dawson, 1996) as does *Albireo whistleri* (Albireonidae) (Barnes, 1984). P218266 and the other odontocete periotics described below possess all of the characters listed above, justifying their assignment to Delphinidae. Table 3 presents comparative measurements of selected dimensions for all delphinid periotics described herein.

Discussion. Within Delphinidae, P218266 is most similar to *Tursiops* and *Lissodelphis*. P218266 is similar to the periotics of *Tursiops* in: (1) its overall size; (2) having the aperture of the internal acoustic meatus opening at the same level as the endocranial surface of the body of the periotic; (3) having a deep internal facial foramen; and (4) having an aquaeductus vestibuli located at the same level as the foramen for the vestibular branch of the vestibulocochlear nerve. P218266

Table 3. Measurements of delphinid periotics from the Whalers Bluff Formation and delphinid periotics from the Red Crag, England. Measurements follow methodology of Kasuya (1973). All measurements are in mm.

	NMV P218264	NMV P218265	NMV P218266	NMV P204352	NMV P218481
Standard length of periotic, from tip of anterior process to posterior end of posterior process, measured on a straight line parallel with cerebral border	28.00	26.66	32.50	29.94	29.40
Thickness of superior process at the level of upper tympanic aperture	11.00	10.00	11.90	12.14	11.58
Width of periotic across pars cochlearis and superior process, at the level of upper tympanic aperture	20.00	17.76	23.00	20.00	19.58
Least distance between the margins of fundus of internal acoustic meatus and of aperture of aquaeductus vestibuli	2.56	2.16	1.58	3.00	2.50
Least distance between the margins of fundus of internal acoustic meatus and of aperture of aquaeductus cochleae	3.00	3.00	3.14	1.50	2.20
Length of the posterior bullar facet	11.00	11.00	11.00	12.46	12.62
Antero-posterior diameter of pars cochlearis	17.00	16.00	17.80	14.66	16.16

differs from *Tursiops* in: (1) the possession of a more acute angle between the anterior process and pars cochlearis; (2) having an aquaeductus cochleae positioned further from the fenestra cochleae, and further dorsally on the endocranial side of the pars cochlearis; (3) having a lower crista transversa; (4) having a poorly developed septum between the tractus spiralis foraminosus and the foramen for the vestibular branch of the vestibulocochlear nerve; and (5) having a less rounded pars cochlearis.

P218266 shares with the periotic of *Lissodelphis*: (1) endocranial surface of the periotic bordering the posterior margin of the internal acoustic meatus, aperture of aquaeductus vestibuli, and aquaeductus cochleae, is uniformly flat; and (2) aperture of the aquaeductus cochleae opens on the same plane as the aperture of the internal acoustic meatus (note that this condition is also seen in *Steno*). P218266 differs from the periotic of *Lissodelphis* by: (1) being markedly larger in overall size; and (2) having a mediolaterally broader aperture of the internal acoustic meatus.

The balance of features noted above indicates that P218266 is a delphinid with close affinities to *Tursiops*. This periotic is not identified as undoubtedly as such due to the subtle differences between P218266 and the periotic of extant *Tursiops* spp. Barnes (1990) provided a thorough review of the fossil record of *Tursiops*. He recognised four fossil species of *Tursiops*: *T. cortesii* Sacco, 1891 (Italy; Late Pliocene, c. 1.75–3.5 Ma, and possibly Early Pliocene, c. 5 Ma); *T. astensis* Sacco, 1891 (Italy; early Late Pliocene, c. 3–3.5 Ma); *T. capellinii* del Prato, 1898 (Italy; middle Pliocene, c. 3.5 Ma); *T. ossenae* Simonelli, 1911 (Italy; middle Pleistocene or late Pleistocene, c. 0.5–0.8 Ma). Other unnamed pre-Pleistocene records of *Tursiops* include: aff. *Tursiops* from the Purisima Formation, California (Late Pliocene, 1.8–3 Ma) (Barnes, 1977); and *Tursiops* sp. from the Yorktown Formation, North Carolina (Early Pliocene, 3.5–4.5 Ma) (Whitmore, 1994).

The record from the Pliocene of Victoria is the first probable pre-Pleistocene fossil record of *Tursiops* from the Southwest Pacific. Furthermore, this fossil occurrence provides corroboration for Barnes' (1990: 18) hypothesis that *Tursiops* has been as geographically widespread during the last six million years as it is at the present time.

Delphinus sp. Linnaeus, 1758 or *Stenella* sp. Gray, 1866

Referred specimen. NMV P218265, virtually complete left periotic (Fig. 7).

Description. P218265 is smaller than P218266 (cf. *Tursiops* sp.) (Fig. 6), closely matching the periotics of both *Delphinus* and *Stenella* in overall proportions. Morphological similarities between P218265 and *Delphinus* include: (1) relatively large diameter of the aperture of the fenestra cochleae; and (2) aperture of the aquaeductus vestibuli is ellipsoid to slit-like in outline and opens posteriorly. However, P218265 differs from *Delphinus* in: (1) the suprameatal area of the periotic, lateral to the aperture of the internal acoustic meatus, is less planar and more convex; (2) the lateral wall of the internal acoustic meatus lacks an elevated platform which obscures the vestibular foramen in endocranial view; (3) the crista transversa is lower; and (4) the aperture of the internal facial foramen is narrower.

Discussion. Whitmore (1994) noted that it is very difficult to distinguish between *Delphinus* and *Stenella* on the basis of periotic morphology. Confounding generic identification of P218265 is the fact that the periotics of *Stenella* show wide individual variation (Kasuya, 1973). In both *Delphinus* and *Stenella*, the aquaeductus cochleae opens at a similar position on the posterior wall of the pars cochlearis. Most preserved features indicate closer affinities with *Stenella* than *Delphinus*. However, all of the identified differences between P218265 and *Delphinus* are subtle, representing differences in degree rather than kind. I do not advocate the definitive placement of P218265 within either *Delphinus* or *Stenella*. In any event, the somewhat intermediate morphology of P218265 between the periotics of *Delphinus* and *Stenella* may indicate that P218265 is from an extinct genus closely related to both of the extant genera in question. In either case, P218265 is the first record of a periotic of the *Delphinus-Stenella* type recorded from the Neogene of Australia.

Fossils representing *Delphinus* or *Stenella* have been recorded from: Upper Member Almejas Formation, Baja California Sur (latest Miocene to Early Pliocene, 3.5–6 Ma) (Barnes, 1998); San Mateo Formation, California (Late

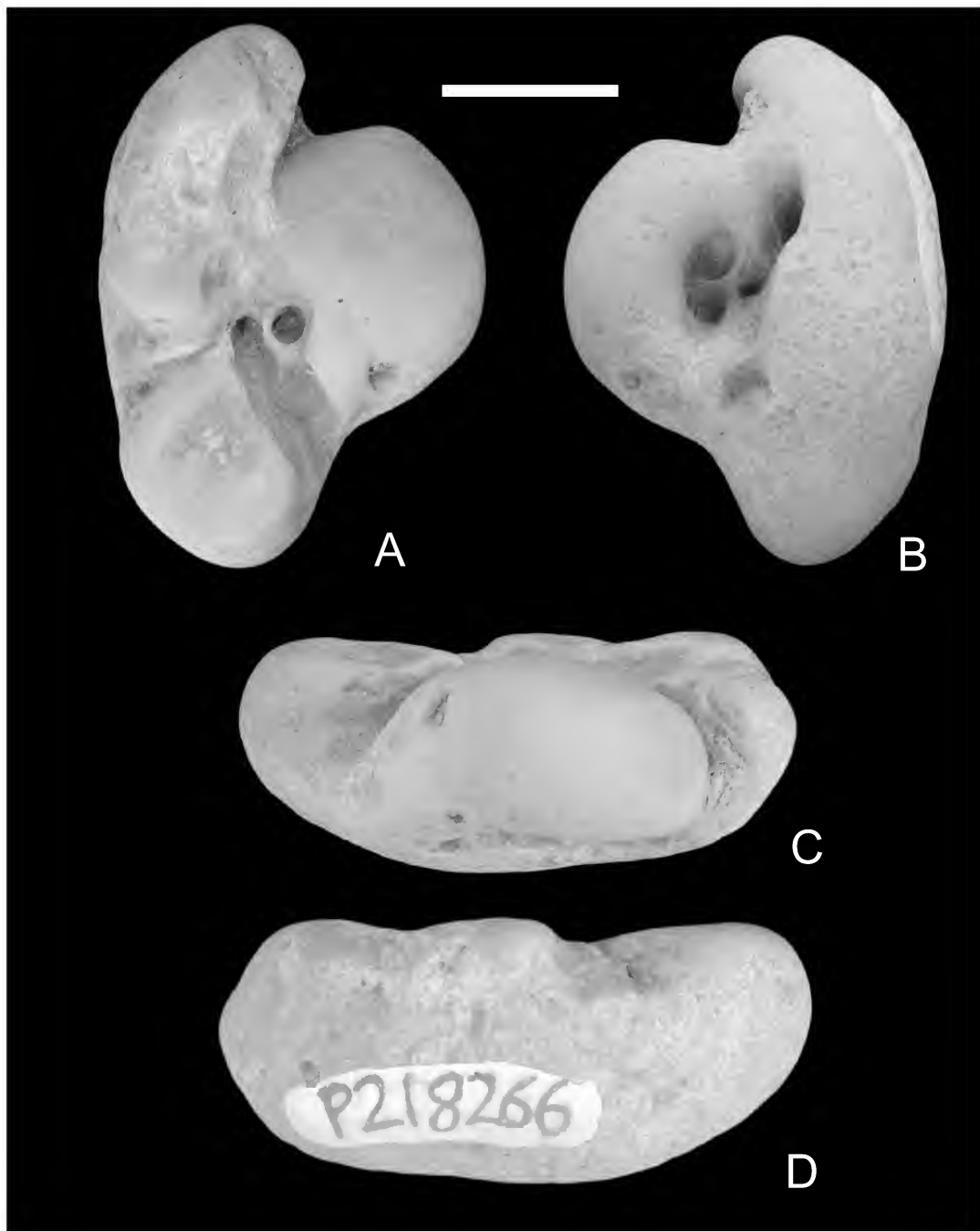


Figure 6. cf. *Tursiops* sp. (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), right periotic, NMV P218266 (AC). **A**, ventral view. **B**, cranial view. **C**, medial view. **D**, lateral view. Scale bar equals 10 mm.

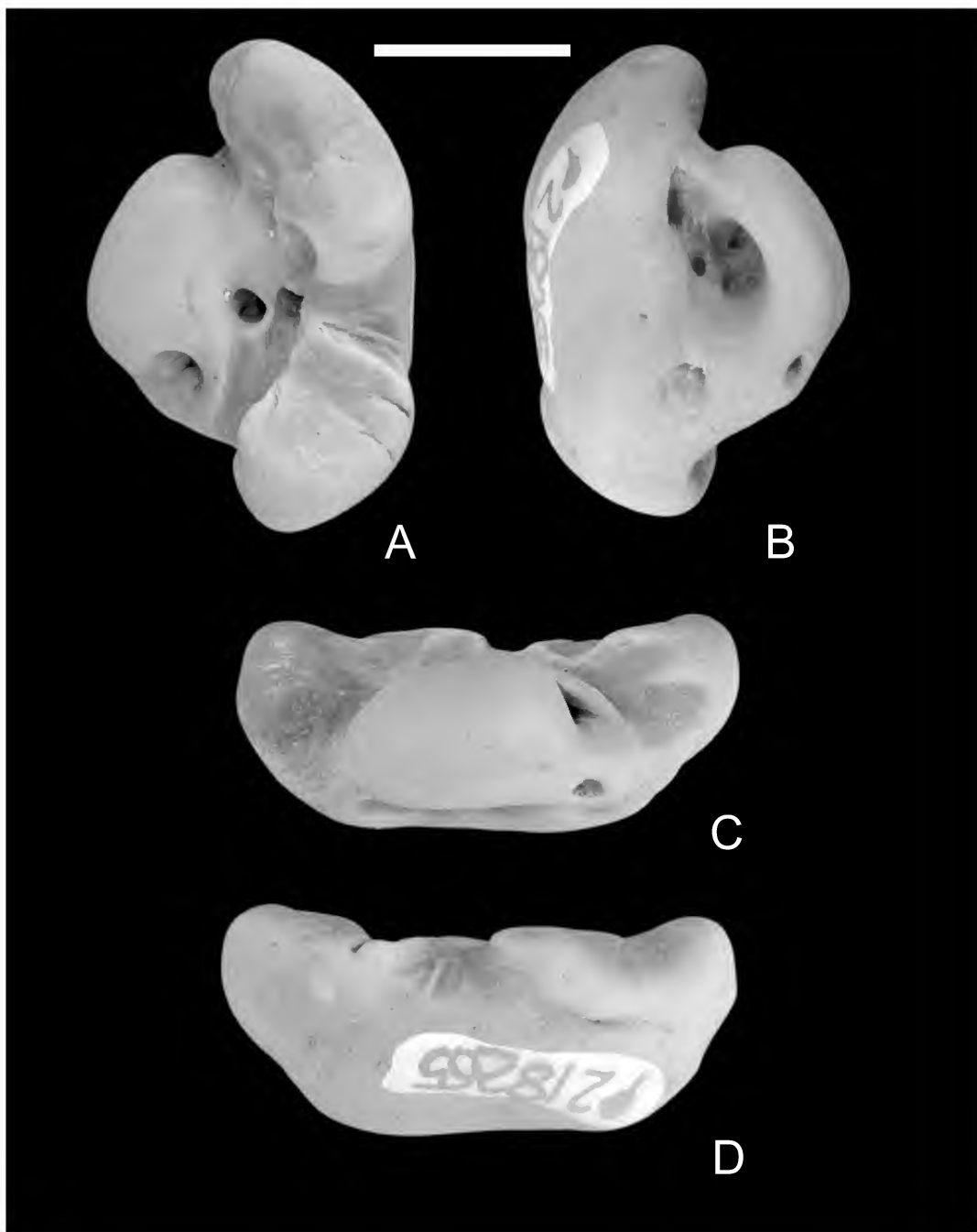


Figure 7. *Delphinus* sp. or *Stenella* sp. (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), left periotic, NMV P218265 (AC). A, ventral view. B, cranial view. C, medial view. D, lateral view. Scale bar equals 10 mm.

Miocene to Early Pliocene, 5–9 Ma) (Barnes et al., 1981); unnamed blue clays at Waihi Beach, Hawera, New Zealand (Early Pliocene, 3–3.6 Ma; Beu, 1995) (McKee and Fordyce, 1987; Fordyce, 1991a: 1262); Yorktown Formation, North Carolina (Early Pliocene, 4.5 Ma) (Whitmore, 1994); Salada Formation, Baja California Sur (Early to Late Pliocene, 3–5 Ma) (Barnes, 1998); Tirabuzón Formation, Baja California Sur (middle Pliocene, 3–4 Ma) (Barnes, 1998); SAO Level of the Pisco Formation, Peru (late Early to early Late Pliocene, 3.0–4.0 Ma) (Muizon and DeVries, 1985; Muizon and Domning, 2002); and San Diego Formation, California (Late Pliocene, 1.8–3.4 Ma) (Barnes, 1973, 1977, 1998).

Genus and species undetermined A

Referred specimen. NMV P218264, virtually complete right periotic (Fig. 8).

Description. P218264 differs from all previously described delphinid periotics from the Pliocene of Portland in its relatively good state of preservation, indicating less post-mortem transport and abrasion, with fine surface details intact. P218264 is distinct from P218265 and P218266 but intermediate in overall size. Notable differences between P218264 and P218265 and P218266 include: (1) a mediolaterally thickened periotic body lateral to the pars cochlearis; (2) apex of anterior process with distinct tubercle; (3) possession of two deep creases in the anteromedial face of the anterior process; (4) aperture of the internal acoustic meatus is mediolaterally compressed, such that in endocranial view the meatus is more ellipsoidal and slit-like in outline than that of either of the others; (5) the aperture of the internal facial foramen is narrow; and (6) the aperture of the aquaeductus vestibuli is so narrow that it appears closed.

Discussion. P218264 does not closely resemble the periotics of any Recent delphinids in the Museum Victoria collections, nor any of the Recent delphinid periotics figured by Kasuya (1973). However, P218264 (Fig. 8) closely resembles two fossil delphinid periotics from the Plio-Pleistocene Red Crag of England (P204352, P218481; Fig. 9). Both periotics were originally identified as *Globicephalus uncidentis* Lankester, 1864 (sensu Lydekker, 1887) by persons unknown. The *Globicephalus uncidentis* periotic figured by Lydekker (1887: plate II fig. 11) probably represents a *Globicephala* periotic, *Globicephalus* being a junior synonym of *Globicephala*. However, P204352 and P218481 (Fig. 9) do not represent *Globicephala* periotics.

An incomplete delphinid periotic (CD 53) has been described from late Neogene sediments of uncertain age on Chatham Island, east of New Zealand (Fordyce and Campbell, 1990). The following features of CD 53 are shared with P218264: well-developed, laterally expanded, parabullary ridge with a globose, tubercle-like anterior apex; anteroventral angle is rounded off; creases in ventrolateral parabullary ridge; and short, broad, fan-like posterior process with heavily fissured posterior bullar facet. Based on these similarities, it is hypothesised that CD 53 is in the same genus, at least, as P218264. Given the Pliocene age of P218264, and Plio-Pleistocene age of P204352 and P218481, this taxonomic assignment of CD 53 suggests a lowest Opoitian (Early Pliocene) or younger age for the Chatham Island delphinid

periotic and its host sediments. Fordyce and Campbell (1990: 62–63) suggested a Late Miocene or younger age for CD 53. Pending the discovery of more complete cranial material including periotics of this type, P218264 is referred to an undetermined genus and species of Delphinidae (as are P204352, P218481 and provisionally CD 53).

Order **Carnivora** Bowdich, 1821

Suborder **Pinnipedia** Illiger, 1811

Family **?Phocidae** Gray, 1821

Genus and species indeterminate

Referred specimens. NMV P218465, incomplete left horizontal ramus of mandible (Fig. 10). NMV P218273, isolated upper incisor or canine tooth (not figured).

Description. P218465 is an incomplete left horizontal ramus with a preserved length of 69 mm, depth at level of dorsal concavity of 21 mm, and mediolateral thickness at level of posterior alveolus for m1 of 10 mm. The surface detail of P218465 is well preserved relative to most of the other marine vertebrate fossils recovered from the Whalers Bluff Formation. P218465 lacks all of the horizontal ramus anterior to the anterior alveolus for p4 and all of the ascending and horizontal rami posterior to the anteriormost corner of the fossa for *m. masseter pars profundus*. No teeth are preserved in situ in the mandible. In overall proportions, the ramus is lightly built. In posterior and dorsal view, slight medial inflection of the ramus is visible. In lateral aspect, there is a small mental foramen located ventral to the position of the interalveolar septum between the anterior and posterior alveoli of p4 (Fig. 10B). This position is almost identical to that of the posteriormost mental foramen on a mandible referred to *Piscophoca* sp. by Walsh and Naish (2002). Such small mental foramina are also present on the mandibles of *Zalophus californianus* Lesson, 1828 (Howell, 1929; pers. obs.). Immediately posterior to the posterior alveolus of m1 is a prominent dorsal concavity 25 mm long (measured from the m1 alveolus to the anterior margin of the fossa for *m. masseter pars profundus*). This dorsal concavity resembles that of *Piscophoca*. The preserved anterior region of the fossa for *m. masseter pars profundus* differs from that of *Piscophoca* in being dorsoventrally broader with a more rounded outline.

P218273 represents an isolated incisor or canine tooth, 28 mm long; its mesiodistal width at a level just below the base of the crown is 8 mm while its buccolingual width at the same level is 6 mm. The crown has smooth enamel and is recurved towards the apex. The root has a consistent thickness and is buccolingually compressed.

Discussion. The pinniped fossils recovered from the Whalers Bluff Formation do not include elements preserving unequivocal synapomorphies of suprageneric pinniped taxa. Berta (1991) and Berta and Wyss (1994) listed the possession of a bony flange below the angular process of the mandible as an unequivocal synapomorphy of Superfamily Phocoidea (sensu Wyss and Flynn, 1993) but the posterior region of the mandible is not preserved in P218465. However, P218465 is tentatively

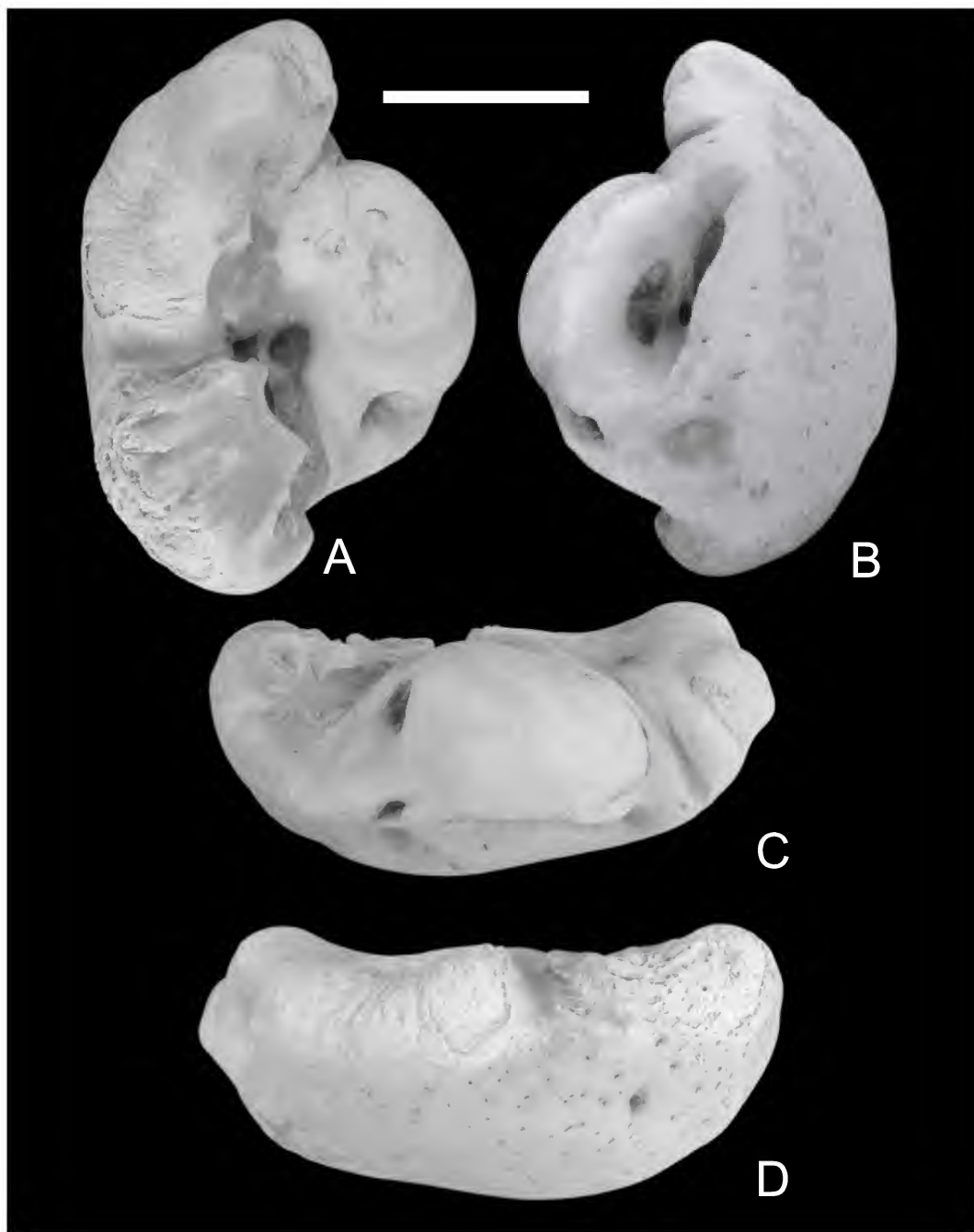


Figure 8. Delphinidae gen. et sp. undet. A (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), right periotic, NMV P218264 (AC). A, ventral view. B, cranial view. C, medial view. D, lateral view. Scale bar equals 10 mm.

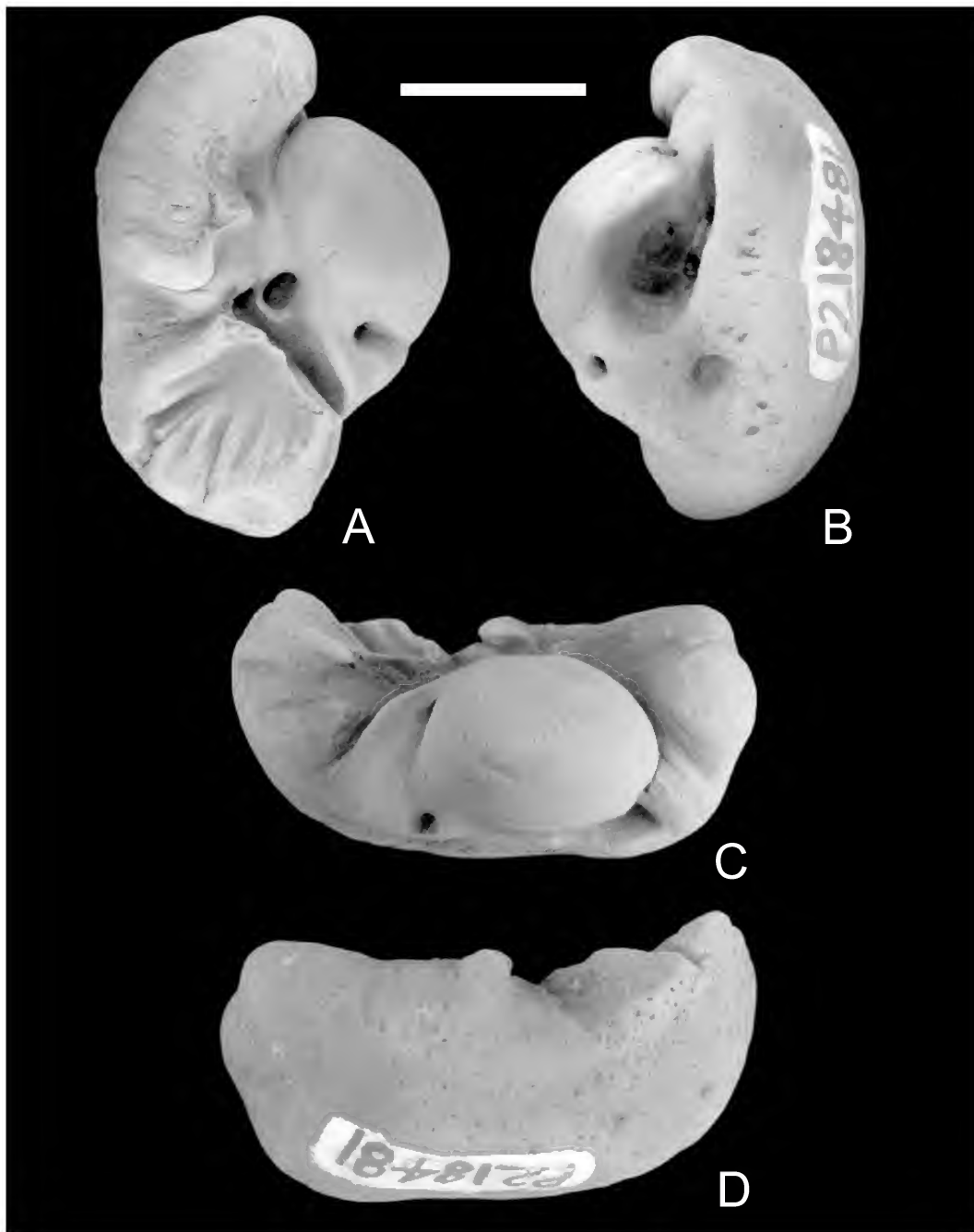


Figure 9. Delphinidae gen. et sp. undet. A (Pleistocene-Pliocene Red Crag, Henley, England), right periotic, NMV P218481 (AC). A, ventral view. B, cranial view. C, medial view. D, lateral view. Scale bar equals 10 mm.

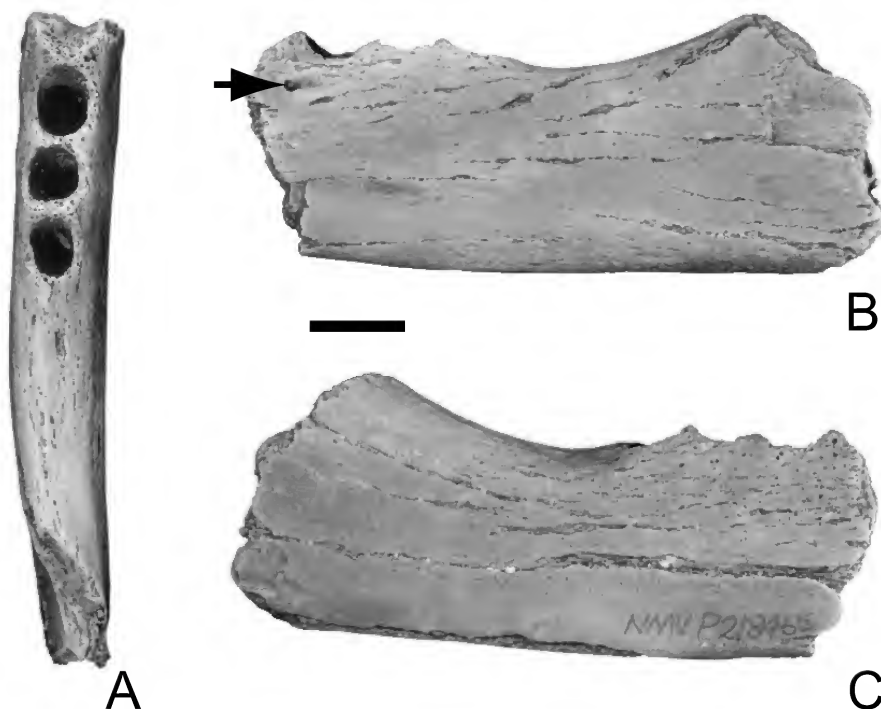


Figure 10. ?Phocidae gen. et sp. indet. (Pliocene Whalers Bluff Formation, Portland, Victoria, Australia), incomplete left mandible, NMV P218465 (AC). **A**, dorsal view. **B**, lateral view. **C**, medial view. Black arrow in **B** points to mental foramen. Scale bar equals 10 mm

referred to the Phocidae on the basis of its morphology and proportions being most similar to the mandibles of phocid seals, as opposed to otariids and odobenids. It remains possible that P218465 represents an otariid mandible. If this were the case, then a major rethinking of otariid evolutionary biogeography would be necessary, as current estimates place the otariid dispersal into the Southern Hemisphere at around the Pliocene/Pleistocene boundary (Deméré et al., 2003; contra Repenning and Tedford, 1977, who indicated a latest Miocene dispersal event at the earliest), and the age of P218465 (and P218273) probably predates that horizon.

Given that P218465 is not similar in morphology to Otariidae but shares certain features with some phocids (see description and discussion below), there is no firm evidence to suggest that the Portland mandible represents an otariid. The fact that phocid seal fossils have previously been reported from Pliocene-aged sediments in Victoria (Fordyce and Flannery, 1983) whereas otariids have not lends further support to the assignment of P218465 to the Phocidae. However, P218465 and P218273 are not referred unquestionably to Phocidae because the late Neogene fossil record of marine mammals in the SW Pacific remains too poorly documented to provide any absolute idea of the composition of the marine mammal fauna during the Pliocene.

Among extant and fossil phocid mandibles, P218465 is

most similar to those of the Pliocene taxa *Acrophoca longirostris* Muizon, 1981, *Homiphoca capensis* Hendey and Repenning, 1972, and *Piscophoca pacifica* Muizon, 1981. P218465 may be clearly distinguished from *Acrophoca*, as it lacks the wide diastema between cheek teeth characteristic of *Acrophoca* (Muizon, 1981). The Portland mandible can be further distinguished from *Homiphoca* (Hendey and Repenning, 1972; Muizon and Hendey, 1980) by the possession of a well-developed dorsal concavity posterior to m1. P218465 is generally very similar to the mandible of *Piscophoca* (Muizon, 1981) in its overall proportions, relative length of the dorsal concavity posterior to m1, subequal diameters of the alveoli and relatively closely spaced alveoli along the tooth row. However, it is not possible at this stage to determine whether the Portland mandible belongs to a species of *Piscophoca* or not.

The Australian fossil record of pinnipeds is currently poor. Fordyce (1991b) summarised the state of knowledge at the beginning of the 1990s, and virtually nothing has been added since that time. The oldest fossil pinnipeds from the SW Pacific are latest Miocene (c. 6 Ma) at the earliest and are from Australia (Fitzgerald, 2004b). Fordyce and Flannery (1983) provided a preliminary assessment of these fragmentary fossils suggesting that they represented monachine phocids. The fossils represent one ?incisor tooth (P16198), two right temporals

(P160399 and P160441), two fused sacral vertebrae (P41759) and an articulated series of eight thoracic vertebrae with five ribs (P160433). None of these specimens has yet been described and only one of the temporals (P160399) has been figured (Fordyce and Flannery, 1983: 99). Recently, two other pre-Pleistocene phocid fossils have been discovered: P42523, isolated right metatarsal V; and P215759, isolated left metatarsal V. Both P42523 and P215759 were derived from beds immediately overlying a phosphatic nodule horizon at the base of the Black Rock Sandstone (Beaumaris, Victoria), and are thus early Early Pliocene in age. The exact relationships of the phocids represented by temporals to extant Monachinae and their fossil sister-taxa (*Acrophoca*, *Homiphoca* and *Piscophoca*) have yet to be determined. The report herein of two probable phocid pinniped fossils from Portland brings the number of known Australian pre-Pleistocene pinniped specimens to nine.

Conclusions

The fossil marine mammal assemblage from the Pliocene-aged Whalers Bluff Formation is the first to be described in detail from Australia. All marine mammal taxa represent members of extant families and for the most part extant genera: *Physeter*, *Tursiops*, and *Delphinus* or *Stenella*. Other taxa, of uncertain affinities below family level, include a balaenid, balaenopterid, a third undetermined genus of delphinid and a phocid pinniped. The diversity of marine mammals in the Portland Pliocene assemblage is impoverished relative to extant faunas, with at least 18 marine mammal species regularly occurring in north-west Bass Strait (Warneke in Menkhurst, 1995; pers. obs.).

Published details of other SW Pacific Pliocene marine mammal assemblages are scanty (Fordyce, 1991a, 1991b; Fitzgerald, 2004b). Only three Australian assemblages provide a reasonable basis for comparison with the Portland Pliocene assemblage; the Beaumaris Local Fauna (Victoria), Grange Burn assemblage (Victoria) and Cameron Inlet assemblage (Flinders Island, Bass Strait). However, only the Cameron Inlet assemblage is approximately contemporaneous with the Portland Pliocene assemblage (about 2.5–4.8 Ma), the Cameron Inlet Formation being late Early to Late Pliocene (about 2.0–4.0 Ma; Fitzgerald, 2004b and references therein). The Beaumaris Local Fauna spans the Miocene–Pliocene boundary, with an age range for the Black Rock Sandstone of about 4.5–5.8 Ma (Dickinson et al., 2002; Wallace et al., 2005). The Grange Burn assemblage is perhaps slightly younger than the Beaumaris Local Fauna, with the Grange Burn Formation being Early Pliocene (>4.35–5.3 Ma) (Dickinson et al., 2002; Fitzgerald, 2004; Wallace et al., 2005). Both the Beaumaris Local Fauna and the Grange Burn assemblage are (at least in part) phosphatic nodule bed deposits.

A significant problem in making meaningful comparisons between the Portland Pliocene assemblage and the other assemblages listed above lies in the great disparity in numbers of specimens collected. Whereas the Portland Pliocene and Cameron Inlet assemblages are known from 30–40 specimens, the Beaumaris Local Fauna and Grange Burn assemblage are known from hundreds of fossils. Nevertheless, with this bias in mind some preliminary comparisons can be made.

In all four assemblages almost all marine mammal families present are extant. The sole exception to this is the occurrence of the paraphyletic family 'Cetotheriidae' (Fordyce and Barnes, 1994; Fordyce, 2003; Geisler and Luo, 1996; Geisler and Sanders, 2003; Kimura and Ozawa, 2002) in the Beaumaris Local Fauna and Grange Burn assemblage (Fitzgerald, 2004b). At the generic level, there appear to be some differences between the known diversity of marine mammals in the Portland Pliocene assemblage/Cameron Inlet assemblage and the Beaumaris Local Fauna/Grange Burn assemblage. In the latter two, extant genera include cf. *Eubalaena*, *Balaenoptera*, *Megaptera*, *Physeter* and cf. *Mesoplodon*. The delphinids from the phosphatic nodule bed assemblages do not appear to be closely related to extant genera, contrary to earlier assessments (e.g., Chapman, 1917). Rather, delphinid periotics and middle ear ossicles from the Beaumaris Local Fauna possess a relatively high number of primitive characters with respect to extant Delphinidae. This is markedly different from the Portland Pliocene assemblage in which most described delphinid periotics seem to represent extant genera. Other apparently archaic aspects of the Beaumaris Local Fauna/Grange Burn assemblage include the high diversity of physeterid taxa (three genera, including a small form similar to the form genus *Scaldicetus* and another similar to *Physeterula dubusii* Van Beneden, 1877) relative to the present (one genus).

The Cameron Inlet assemblage appears to be essentially modern in aspect based on fossils recovered to date. Fordyce (1991b: 1183) listed ziphiids (including *Mesoplodon* sp., based on isolated periotics), physeterids (cf. *Physeter macrocephalus*) and balaenopterids in this assemblage. Fitzgerald (2004: 198) included cf. *Balaenoptera*, cf. *Megaptera* and a possible delphinid. Sutherland and Kershaw (1971) reported an incomplete skull (NMV P23961) as *Ziphius* sp. but Fordyce (1984b: 939) later questioned this assignment and re-identified NMV P23961 as *Mesoplodon* sp. The Cameron Inlet assemblage is generally similar to the Portland Pliocene assemblage which is perhaps not unexpected given their similar geological age and geographic proximity.

It has previously been noted that latest Miocene through Pliocene marine mammal assemblages across the globe include extinct, often aberrant, genera and families and formerly wider (in some cases unexpected) geographic ranges for extant taxa that today have restricted geographic distributions (Fordyce et al., 2002 and references therein). Indeed, the apparently recent evolution of marine mammal faunas of modern aspect led Fordyce and colleagues (2002) to suggest that among cetaceans at least a major ecological change occurred about 3–4 million years ago. This change is marked by the last appearance in the fossil record of genus and family-level taxa displaying relatively primitive grades of evolution (e.g., Albireonidae, *Herpetocetus*; Barnes, 1984; Whitmore, 1994; Oishi and Hasegawa, 1995; Barnes and Furusawa, 2001; Fordyce and Muizon, 2001) as well as novel morphological adaptations and inferred palaeoecology (e.g., Odobenocetopsidae, *Australodelphis*; Fordyce et al., 2002; Muizon and Domning, 2002).

The early Pliocene is marked by a global warming trend beginning at c. 4.5–5.5 Ma with the rapid development of full-scale Northern Hemisphere and Antarctic glaciation occurring

in the late Pliocene at approximately 2.75–3.2 Ma (Zachos et al., 2001; Ravelo et al., 2004; Wara et al., 2005). Gallagher and colleagues (2003) presented data indicating that the earlier Pliocene (3.1–5.3 Ma) was a time of generally stable marine temperatures in Bass Strait with surface temperatures perhaps as much as 3°C warmer than today (Ravelo et al., 2004). The Late Pliocene in Bass Strait was characterised by a fluctuating, overall cooler climate than the preceding Early Pliocene (Gallagher et al., 2003). As Fordyce and colleagues (2002) have indicated, climatic and oceanic changes associated with rapid global cooling at c. 3.2 Ma were likely major influences on the evolution of the modern marine mammal fauna. A larger sample of marine mammal fossils from Pliocene-aged assemblages in south-east Australia with finer resolution of stratigraphic distribution of marine mammal taxa during the Pliocene is required for more detailed correlations between Pliocene marine mammal and climatic evolution.

The description of the Pliocene marine mammal assemblage from Portland alleviates the dearth of information on SW Pacific marine mammal assemblages during the late Neogene. The occurrence of extant cetacean taxa (*Balaenoptera*, *Physeter*, *Delphinus/Stenella* and *Tursiops*) in the Whalers Bluff Formation (>2.5–4.8 Ma) (and Cameron Inlet Formation) indicates that the marine mammal fauna off south-east Australia had begun to take on a modern aspect by at the earliest 4.8 Ma and latest around 2.5 Ma. Indeed, most of the cetacean species still exist in the seas off Portland (Warneke in Menkhurst, 1995; pers. obs.). That the latter cetacean taxa occur in Early-Late Pliocene deposits in the SW, SE and NE Pacific, and NW Atlantic, suggests that several extant cetacean genera were widespread in the world's ocean basins prior to about 2.5 Ma.

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Two new Middle Miocene spatangoids (Echinoidea) from the Murray Basin, South Australia

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Abstract

Holmes, F.C., Ah Yee, C., and Krause, J. 2005. Two new Middle Miocene spatangoids (Echinoidea) from the Murray Basin, South Australia. *Memoirs of Museum Victoria* 62(1): 91–99.

Two new spatangoid taxa are described from the Glenforslan Formation cropping out in the Murray River cliffs near Blanchetown, South Australia. One taxon, *Murraypneustes biannulatus* gen. et sp. nov., a large species of spatangoid with two 'peripetalous' fascioles (one circling the margin and the other close to the distal end of the relatively short petals), two distinct sizes of aboral primary tubercles, and a depressed apical system. The other spatangoid described, *Spatagobrissus dermodyorum* sp. nov. differs from the only other fossil species of this genus recorded from Australia, *S. laubei* (Duncan, 1877), in having a much shorter labrum, markedly larger peristome and periproct and larger primary tubercles within the peripetalous fasciole.

Keywords

Echinoidea, Spatangoida, *Murraypneustes*, *Spatagobrissus*, new taxa, Middle Miocene, South Australia

Introduction

Of all the Australian Tertiary sedimentary sequences that contain extensive echinoid faunas, the 150 km of Murray River cliffs, from Overland Corner, east of Waikerie, to Murray Bridge, South Australia, have over the last 120 years been more comprehensively studied by palaeontologists, students and amateur collectors than any other similar area. In the Miocene stratigraphic sequences along the Murray River and elsewhere in Australia, species belonging to the Spatangoida constitute approximately 50 percent of the recorded taxa of irregular echinoids. In view of the number of spatangoids occurring in this section of the Murray River cliffs, the discovery in 2003 of three specimens of a new genus belonging to this order, seemingly unrelated to any other genus known from the continent's fossil record, was unexpected.

The specimens were found within 300 m of each other in a single bed of the Glenforslan Formation, cropping out on the left bank of the Murray River, 7 km NNE of Blanchetown, South Australia [Museum Victoria locality PL3203]. Further investigation of the surface exposure of the formation in the general vicinity of this discovery failed to produce any additional specimens of the new genus.

Materials and methods. Specimen numbers prefixed P, on which the studies are based, are housed in the Invertebrate

Palaeontology collection, Museum Victoria (NMV). In addition to type material, the new species of *Spatagobrissus* is represented by several specimens in private collections. Measurements were made with a dial calliper to an accuracy of 0.1 mm. Parameters are expressed as a percentage of test length (%TL) or test width (%TW).

Age and stratigraphy

The Glenforslan Formation, synonymous with the Lower Morgan limestone, conformably overlies the Finniss Formation and is of early Middle Miocene (Batesfordian, Langian) age. The thickness of the unit is relatively consistent at 13–15 m although this is reduced in southern exposure due to post-Middle Miocene uplift and subsequent erosion. The formation is sublithified to lithified, weathering to whitish-cream colour in outcrop (Lukasik and James, 1998). It is composed of cycles of mollusc-bryozoan floatstone, with a microbioclastic packstone matrix, grading upward into *Celleporaria* rudstone tops (infaunal bivalve and gastropod-rich microbioclastic matrix with large branching and sheeted *Celleporaria*) which also contain pectens and oysters. Echinoids tend to be found at or above the rudstone-floatstone contact at the base of the cycles, the latter containing delicate branching and uni-laminar sheet bryozoans of 1–3 cm length. Sediments are pervasively mottled, obscuring all physical sedimentary textures. The middle

Glenforslan Formation is interpreted as being deposited in relatively shallow waters, possibly less than 10 m, based on the presence of calcareous algae and mixotrophic foraminifers (Lakasik, pers. com. 2005). It forms part of the richest warm-water biotic record from southern Australia at a time of maximum transgression of the sea across the continental shelf (McGowran and Li, 1994, and papers cited therein).

The three specimens of the new genus were found about 7.4 m above the base of the formation, approximately 2 m above the *Lepidocyclus* Zone.

Associated fauna

Nineteen species of echinoids have been recorded from the Glenforslan Formation within 500 m upstream and downstream of PL3203 (Table 1), compared with 28 confirmed species known to occur within the Morgan Group (Glenforslan, Cadell, and Bryant Creek Formations).

Table 1. Echinoids recorded within the vicinity of locality PL3203. Letters in brackets indicate the frequency of occurrence of each species. [A], abundant; [C], common; [F], fairly common; [U], uncommon; [R], rare. References to authors and supporting literature cited below, but not listed in the main text references, can be found in Holmes (1993).

Cidaroida

Goniocidaris murrayensis Chapman and Cudmore, 1934 [C]

Arbacoidea

Murravechinus paucituberculatus (Gregory, 1890) [F]

Temnopleuroidea

Cryptechinus humilior (Bittner, 1892) [C]

Ortholophus morganensis Philip, 1969 [C]

O. pulchellus (Bittner, 1892) [C]

Clypeasteroidea

Monostychia australis Laube, 1869 [A]

M. sp. 'C' in Holmes, 1999 [F]

Scutellinoides patella (Tate, 1891) [C]

Spatangoida

Brissopsis tatei Hall, 1907 [U]

Brissus sp. nov? [R]

Cyclaster archeri (Tenison Woods, 1867) [C]

Eupatagus rotundus Duncan, 1877 [U]

Eupatagus sp. indet. [U]

Hemiasster (Bolbaster) planedeclevis Gregory, 1890 [C]

Lovenia cf. *forbesi* (Tenison Woods, 1862) [C]

Murraypneustes biannulatus gen. et sp. nov. [R]

Pericosmus compressus (Duncan, 1877) [R]

Protenaster antiaustralis (Tate, 1885) [U]

Spatagobrius dermodyorum sp. nov [F]

Systematic Palaeontology

Order **Spatangoida** Claus, 1876

Suborder **Micrasterina** Fisher, 1966

Family ***Incertae sedis***

Remarks. The combination of generic features, particularly the presence of a marginal 'peripetalous' fasciole, intermittent horizontal fasciole bands and a rudimentary non re-entrant

peripetalous fasciole clear of the distal ends of paired petals, clearly distinguish the new genus *Murraypneustes* from virtually all other taxa assigned to the Micrasterina, in particular the 22 genera included in the Asterostomatidae Fisher, 1966. Only one of these genera, *Asterostoma* Agassiz, 1847, has tentatively been retained in the Asterostomatidae (together with *Stomaporus* Cotteau, 1888, a genus originally assigned to the Brissidae Gray, 1855) by Smith et al. (2003). Of the remaining 21 genera, Smith et al. have conditionally reassigned 13 to other families, only six of which are included in the Micrasterina. The remaining eight are listed as *incertae sedis* or as belonging to an unnamed taxon. Until a detailed revision of these latter genera is published, it is considered imprudent to assign the new genus to a specific family.

Murraypneustes gen. nov.

Type and only known species. *Murraypneustes biannulatus* sp. nov.

Diagnosis. Large ovoid spatangoid with centrally depressed adapical surface, apex well posterior of centre. Apical system ethmolytic with 4 gonopores. Aboral primary tubercles of 2 distinct sizes, small and randomly spaced, the larger proximal to the ambitus. Labrum long, narrow, partially tuberculate, extending to third ambulacral plate. Two 'peripetalous' fascioles present; one marginal, passing above the periproct (pseudolateral); the second, rudimentary, non re-entrant and clear of the distal ends of paired petals. Intermittent horizontal fasciole bands also occur between the 2 'peripetalous' fascioles. Subanal fasciole in contact with marginal periproct.

Etymology. For the Murray River cliffs, the origin of the fossils, and "pneustes", a common suffix used for spatangoid echinoids. Gender masculine.

Remarks. The following analysis of morphological features of genera similar to *Murraypneustes* gen. nov. is based primarily on Mortensen (1950a) and Smith et al. (2003). Although approximately 30 genera within the Micrasterina have been investigated, only eight warranted further scrutiny; four currently unassigned to a family by Smith et al. (2003), *Elipneustes* Koehler, 1914, *Eurypatagus* Mortensen, 1948, *Linopneustes* A. Agassiz, 1881, and *Platybrissus* Grube, 1865; three belonging to the Maretiidae (Lambert, 1905), *Eupatagus* L. Agassiz, 1847, *Mazzettia* Lambert and Thiéry, 1915 and *Spatagobrius* H. L. Clark, 1923; and Macropneustidae genus *Lajanaster* Lambert and Sanchez Roig, 1924.

Using a broad comparison of 38 features, *Linopneustes* stands out from the other seven genera as having closest affinity with *Murraypneustes*; four of its recorded six species, *L. longispinus* (A. Agassiz, 1878), *L. fragilis* (de Meijere, 1903), *L. spectabilis* (de Meijere, 1903), and *L. brachipetalus* Mortensen, 1950b having distinct marginal peripetalous fascioles passing above the periproct. In the other two, *L. murrayi* (A. Agassiz, 1879) and *L. excentricus* de Meijere, 1903, the peripetalous fasciole is not marginal but somewhat higher up on the test (Mortensen, 1950a: 221). Although *L. fragilis* has multiple fasciole bands around the ambitus,

L. murrayi a rounded margin (Smith, pers. com. 2005) and *L. longispinus* relatively short closing petals; *Murraypneustes* is distinguished by its centrally depressed aboral surface forming four apices (domed on *Linopneustes*) with the highest point of the test posterior to the apical disk (anterior in *Linopneustes*), the presence of two 'peripetalous' fascioles and intermittent horizontal fasciole bands, two distinct sizes of small randomly spaced aboral primary tubercles, the larger restricted to the area outside the upper 'peripetalous' fasciole, and a prominent angular subanal fasciole.

Based on the same criteria, three other genera show a moderate degree of morphological similarity to *Murraypneustes*, namely *Elipneustes*, *Mazzettia*, and *Eupatagus*.

Elipneustes, however, can be distinguished by its very long, parallel-sided, open-ended, flush petals with conjugate pore pairs; single, narrow, marginally situated peripetalous fasciole; peristome situated immediately below the apical disk; small thickset plastron with minimal posterior swelling; and much larger primary tubercles scattered over all the aboral interambulacra.

Mazzettia, a poorly known fossil genus, has an elongated heart-shaped test with a low sharp margin, very long weakly-bowed petals closing distally, no recorded peripetalous fasciole and only occasionally a weak shield-shaped subanal fasciole, an elongated labrum just reaching the relatively small plastron, and random but closely spaced coarse tubercles aborally.

Eupatagus, although possessing well developed peripetalous and subanal fascioles is easily categorised by its lack of an anterior sulcus, predominately short lanceolate closed petals, primary tubercles of varying density restricted to the area within the peripetalous fasciole in aboral interambulacra 1–4, and very small evenly spaced tubercles distally over the remainder of the aboral surface. Comparison of other features is difficult because of variability among the very large number of described species. In particular, the eight Australian fossil species vary considerably in profile, are generally more rounded, and have an extremely wide range of primary tubercle densities when compared with the type species on which the generic description is based.

Two other genera, *Platybrissus* and *Eurypatagus*, are distinguished by their complete lack of fascioles, although the former may have a subanal fasciole present in juvenile specimens.

Lajanaster, although depressed aborally, has no anterior sulcus, a relatively sharp ambitus, a markedly narrow plastron, and primary tubercles confined to the posterior column of anterior and lateral interambulacra within the peripetalous fasciole.

Spatagobrissus was included in the comparative analysis, primarily as a new species of the genus occurs at the same locality (PL3203) as *Murraypneustes*. In most respects the former is very similar to *Eupatagus* but has shorter petals and only small tubercles over the whole of the aboral surface.

Murraypneustes biannulatus. sp. nov.

Figures 2A–F, 3A–C, 4A, B, 5

Type material. Holotype, NMV P312370 from early Middle Miocene Glenforslan Formation (Batesfordian), Morgan Group, 7 km NNE of

Murray River Lock 1, Blanchetown, South Australia [NMV locality PL3203].

Paratypes, NMV P312371 and P312372 from the same location.

Diagnosis. As for genus.

Description. Test moderately large, ovoid in outline with shallow anterior sulcus and pointed, slightly truncated posterior. Specimens range from 72 to 81 mm in length, with maximum width 81–86%TL occurring at 45%TL from anterior ambitus. Test 44.1%TL high (uncompressed specimen) with apex of all specimens well posterior of centre, 63–67%TL from anterior ambitus.

Centre of test on adapical surface depressed around apical disk and proximal end of paired petals to form minor apices in interambulacra 1, 4 and 5, and conjointly, a raised area across ambulacrum III and interambulacra 2 and 3. Adoral surface mildly concave in vicinity of peristome with ambulacrum III slightly recessed anteriorly and the plastron forming a fairly pronounced keel posteriorly, terminating at the anterior edge of the subanal fasciole.

Primary tubercles on adapical surface of 2 distinct sizes, both widely and randomly spaced. Larger of the two restricted to the distal 35% of the radius on interambulacrum 5, and 25% elsewhere. Adorally, larger primary tubercles closely and evenly spaced throughout, with exception of naked areas in ambulacra I and V and phylloids plates of ambulacra II, III and IV. Overlapping scrobicules on adoral surface form distinct diagonal ridges. Small tubercles closely spaced immediately below ambitus increase in size to that of larger primary tubercles below curvature of margin. Large primary tubercles, perforate with undercut mamelon and crenulated platform, and maximum scrobicular diameter of approximately 2.5 mm, twice size of smaller counterparts. Ring of scrobicular tubercles not always present.

'Peripetalous' and subanal fascioles present, the former, though not continuously visible on any specimen clearly passes above periproct, while latter is distinctly angular, forming hexagonal outline where in contact with lower edge of periproct. Intermittent horizontal fasciole bands also present laterally above and parallel to marginal 'peripetalous' fasciole. Uppermost very narrow and more continuous fasciole, although clear of distal ends of petals, appears to be a rudimentary peripetalous fasciole not indented interradially (Fig. 3).

Apical system anterior of centre, 39.5–42.2%TL from anterior ambitus to centre of disk, level or slightly below proximal end of paired petals. Ethmolytic, with 4 small closely spaced gonopores approximately 0.3 mm in diameter, anterior pair closer together than posterior pair. Detail of ocular plates indeterminate. Hydopores numerous, approximately 70 visible in one specimen, centrally located but extending between posterior pair of gonopores and possibly ocular plates I and V (Fig. 4A, B).

Petals lanceolate, moderately wide at midlength, closed distally, situated in gentle concave depressions incorporating adradial edges of adjacent interambulacra and continuing proximally across apical disk. Anterior paired petals shorter than posterior pair, extending on average 60% of the radius measured along the surface of the perradial suture from centre of

apical disk to ambitus; posterior pair about 56% radius. Inner pores of petals oval, outer pores slot-like, slightly curved and 50% wider. Pore pairs not conjugate but linked by a fine ridge which extends along both sides of each pore (Fig. 5). Maximum width of interporiferous zone slightly more than twice width of poriferous zone. Anterior paired petals diverge at approximately 135° and contain on average 23 pore pairs, posterior petals 297° and 26 pairs. Secondary tubercles extend randomly across interporiferous and poriferous zones and for a distance outside petals without primary tubercles. Ambulacrum III not petaloid, basically flush with adjoining interambulacra for about 50% radius, then gradually becoming concave towards anterior sulcus. Other details unknown, no sign of pores or regularly spaced tubercles being visible on specimens.

Peristome reniform, centre situated 27–30%TL from anterior ambitus, longitudinal dimension approximately 6.5%TL, transverse dimension 12%TL. Phyllodes short and not particularly well developed.

Labrum long and narrow, averaging 20.5%TL, slightly curved at junction with peristome and abutting the plastron at centre of third pair of adjacent ambulacral plates. Numerous small tubercles adjacent to peristome with a few larger ones towards the posterior end (Fig. 2C).

Plastron closely tuberculate, width approximately 75% length measured from posterior edge of labrum to anterior edge of subanal fasciole. Strong posterior taper suggests sixth and subsequent plates of ambulacra I and V indent behind paired episternal plates.

Periproct opening marginal, not visible from above, tear shaped, slightly wider than high, set in a slight truncation approximately 65° to the horizontal.

Etymology. *biannulatus* (L) – two-ringed, referring to the presence of two ‘peripetalous’ fasciole rings.

Family Maretiidae

Spatagobrissus H. L. Clark, 1923

Type species. *Spatagobrissus mirabilis* H. L. Clark, 1923, by original designation.

Diagnosis. See H. L. Clark (1923: 402)

Spatagobrissus dermodyorum sp. nov

Figures 6A–E, 7A–C, 8A–E

Type Material. Holotype. NMV P312570 from early Middle Miocene Glenforslan Formation (Batesfordian), Morgan Group, in the vicinity of NMV locality PL3203, 7 km NNE of Murray River Lock 1, Blanchetown, South Australia.

Paratypes, NMV P312571–P312373 from the same general area. Other material used for statistical purposes is held in Museum Victoria and private collections.

Description. Test small, subcircular in outline with minimal posterior truncation and no anterior sulcus. Specimens range 30.0–45.5 mm in length with maximum width 82–90%TL occurring 51–58 %TL from anterior ambitus. Maximum height 49.5–60%TL at 52.6–65.5%TL from anterior ambitus. Adapical surface moderately inflated, evenly curved

transversely above well-rounded margin with ambitus situated at about 30%TH. Adoral surface very mildly convex but with prominent posterior keel caused by sharp rise of ambulacra I and V posterior to centre. In lateral view, posterior truncation covers about 35%TH.

Apical system ethmolytic with 4 genital pores, centre 31.3–38.6%TL from anterior ambitus (Fig. 7A). Paired petals short (26.5–32.5%TL measured along surface of perradial suture from centre of apical disk), narrow (7.0–9.0%TL), lanceolate, closing to closed, posterior pair marginally longer than anterior pair. Anterior pair diverge at about 135° , posterior pair 310° . Pore pairs conjugate, inner pores oval, outer-tear shaped. Anterior row of pore pairs in anterior paired petals distinctly narrower than posterior row and atrophied adapically. Interporiferous zone up to 1.5 times width of poriferous zone at widest point. Ambulacrum III flush adapically, with 2 rows of indistinct longitudinally orientated pore pairs and interporiferous zone containing few secondary tubercles and numerous miliaries.

Peripetalous fasciole subcircular, not indented. Numerous small, randomly spaced perforate, crenulate, primary tubercles occur in interambulacra within fasciole. Outside fasciole, tubercles in posterior half of test very small, but anterior to centre, gradually increasing in size towards interambulacra 2 and 3.

Peristome reniform, mildly sunken, width 16.0–19.3%TL, length 8.9–10.3%TL with anterior border 23.4–26.8%TL from anterior ambitus. Phyllodes moderately developed with slot-shaped pores in circular depressions. Labrum short and wedge-shaped extending only to centre of second pair of adjacent ambulacral plates. Anterior edge raised above surrounding ambulacra and slightly projecting over peristome. Miliary tubercles present with few secondary tubercles in anterior half (Fig. 7B).

Plastron long, width about 55–60% length, with ambulacral plates indenting posteriorly. Subanal fasciole circular to transversely oval, enclosing 3 pore pairs each side of interradian suture, and with slight anterior projection at posterior end of prominent plastral keel. Posterior edge of fasciole marginally clear of periproct opening. Adorally, ambulacra I and V relatively wide, covered with very fine, randomly spaced miliary tubercles up to sixth plate, then by tubercles of similar size to rest of adoral surface.

Periproct, tear-drop shaped, generally positioned vertically on truncated posterior margin but slightly visible from above on some specimens; height 17.1–19.1%TL, width 13.2–16.0%TL.

Etymology. Named for Michael and Marie Dermody, owners of Glenforslan Station.

Remarks. *Spatagobrissus dermodyorum* sp. nov. differs primarily from the Middle Miocene Port Campbell Limestone species, *Spatagobrissus laubei* (Duncan, 1877), in having narrower test with more posterior maximum width (Fig. 8A), markedly larger peristome and periproct (Fig. 8D, E), and very much shorter labrum (Fig. 8B). In addition, anterior paired petals are shorter and posterior petals longer (Fig. 8C), with divergent angle of latter greater than *S. laubei*. Aboral primary

tubercles larger within peripetalous fasciole and interambulacra 2 and 3, while fine tubercles outside fasciole on posterior half of test are much smaller in diameter. Adorally, plastron wider and longer, and ambulacra I and V narrower.

The extant type species *Spatagobrissus mirabilis* is characterised by a larger (up to 110 mm long) and less inflated test, more posteriorly located apical system in line with maximum width, greater area enclosed by peripetalous fasciole, shorter peristome, and periproct situated on an obliquely truncated surface below the ambitus. Primary tubercles within the peripetalous fasciole of *S. mirabilis* are also larger and more closely spaced than in *S. dermodyorum*.

Spatagobrissus incus Baker and Rowe, 1990, an extant species endemic to southeast Australian waters, particularly between Flinders Island (Tasmania) and western Spencer Gulf, South Australia, has a larger and more rounded test (up to 80 mm long) and, similar to *S. mirabilis*, more posteriorly located apical system and greater area enclosed by peripetalous fasciole.

Compared with *S. dermodyorum*, it also has a much wider and longer plastron and narrower adoral ambulacra I and V. Miskelly (2002: 156) noted two pairs of pore pairs occur in each side of the subanal fasciole, a feature also recorded for *S. laubei* (McNamara et al., 1986: 80). This contrasts with the three pairs found on *S. dermodyorum* (Fig. 7C).

Discussion

The major diagnostic features of *Murraypneustes*, particularly the position of the two 'peripetalous' fascioles, the intermittent horizontal fasciole bands, and the random pattern and separation of two distinct sizes of primary tubercles across the aboral surface, give little indication of its lineage. Certainly, within the Australian Cenozoic sequences that predate the early Middle Miocene Glenforslan Formation, all the 13 recorded genera of Micrasterina have their peripetalous fasciole close or in contact with the paired petals. Only the brissid *Cyclaster* is recorded as having developed multiple fascioles in some specimens (McNamara et al., 1986: 68).

Similarly, there are no extant genera in Australian waters that have any specific combination of characters that link them to *Murraypneustes*. Even the extant species *Linopneustes brachypetalus*, found off the east coast of Australia, has long petals in contact with its marginal peripetalous fasciole.

The lack of any juvenile specimens of the new genus, or indeed any marked variation in the size of the three known specimens, precludes any useful comment on the disposition and specific function of its somewhat unusual arrangement of fascioles, as such development takes place at a very early stage of ontogeny.

Excluding *Murraypneustes*, only *Hemiaster*, of the nine spatangoid genera known to occur in the Glenforslan Formation sequence which embraces locality PL3203 (Table 1), has no extant record in Australian waters. The eight remaining genera are today almost exclusively benthic filter feeders, living inshore or on the continental shelf. Five, *Brissopsis*,

Brissus, *Cyclaster*, *Lovenia* and *Pericosmus*, occur in tropical waters, and three, *Eupatagus*, *Protenaster* and *Spatagobrissus* in temperate waters (Rowe and Gates, 1995). Species of these eight extant genera, with the possible exception of *Cyclaster*, are known to occur at depths of less than 20 m in Australian or New Zealand waters. This depth range is consistent with the sedimentary deposition of the Glenforslan Formation. On the other hand, Indo-Pacific species of *Linopneustes*, including *L. brachypetalus*, are found at depths exceeding 270 m (range 272–1788 m), with only the West Indies species, *L. longispinus*, extending up into sublittoral waters (70–570 m) (Mortensen, 1950a).

Based on the available evidence, it is reasonable to assume *Murraypneustes dermodyi* was a benthic filter feeder inhabiting relatively shallow, warm (?sub-tropical) waters.

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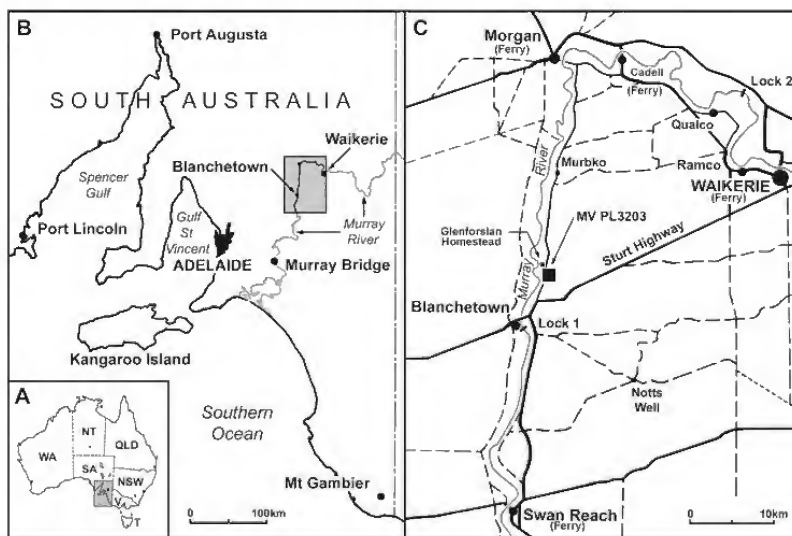


Figure 1. A, B, general location maps; C, map of the Murray River between Waikerie and Swan Reach, South Australia, showing locality of NMV locality PL3203, north of Blanchetown.

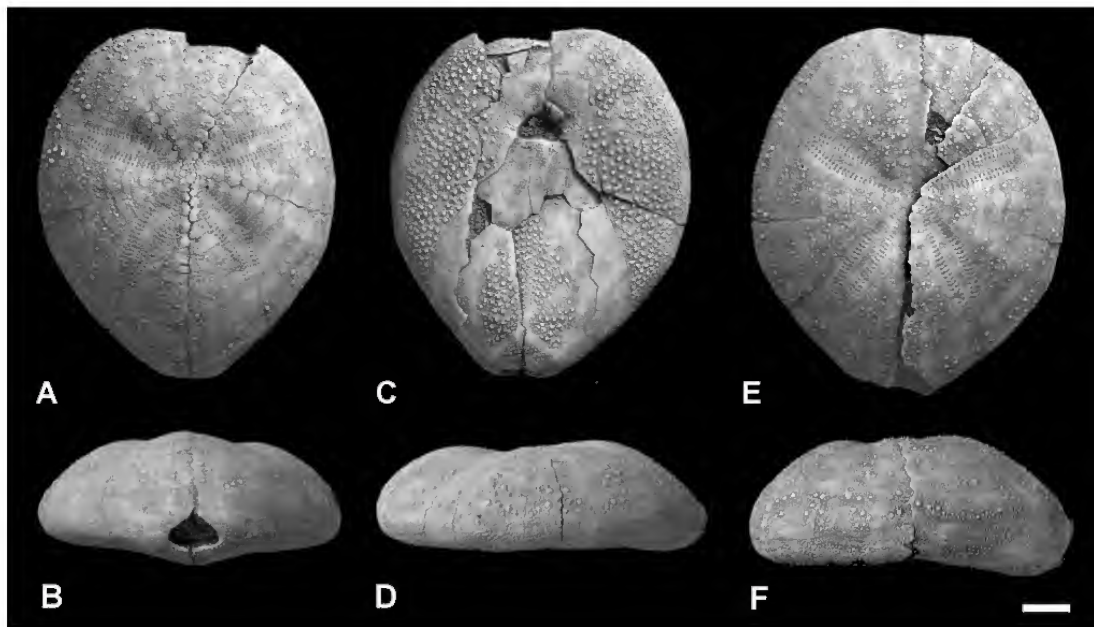


Figure 2. *Murraypneustes biannulatus* gen et sp. nov. A–D, adapical, posterior, adoral and left lateral views of holotype NMV P312370; E, adapical view of paratype NMV P312371; F, left lateral view of paratype, NMV P312372. All from the early Middle Miocene Glenforslan Formation in the vicinity of NMV locality PL3203, north of Blanchetown, South Australia.

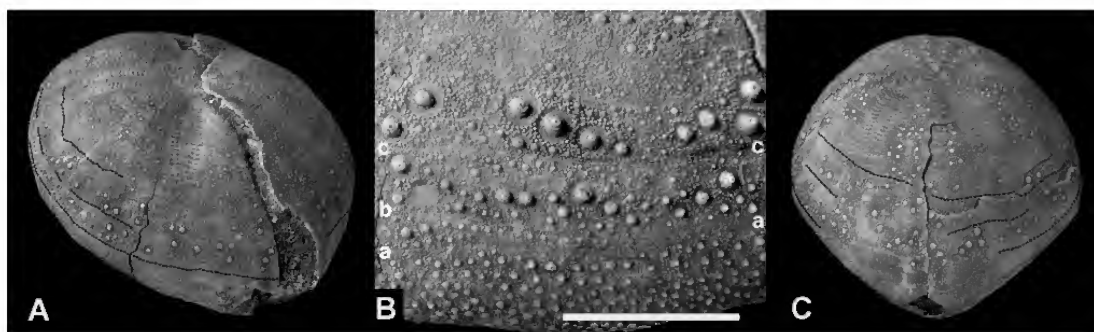


Figure 3. Fasciole details of *Murraypneustes biannulatus* gen. et sp. nov. A, B, oblique lateral view and ambulacrum IV detail above margin of paratype, NMV P312371; C, oblique posterior view of paratype, NMV P312372. Scale bar 10 mm.

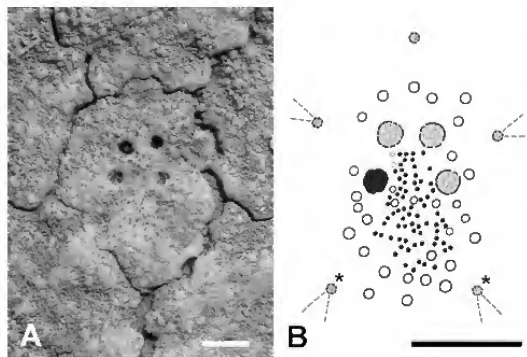


Figure 4. Apical disk details of *Murraypneustes biannulatus* gen. et sp. nov. A, holotype NMV P312370; B, drawing of paratype, NMV P312372, showing extent of hydropores (black circles), tubercles (white circles), and gonopores and oculars (black or stippled). Location of posterior oculars (marked *) is assumed. Scale bars 1 mm.

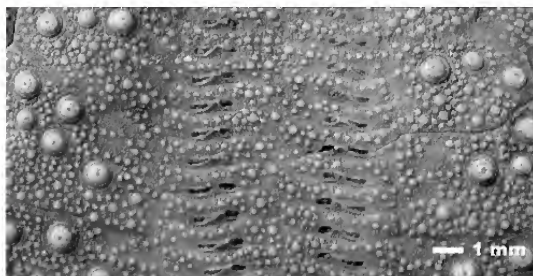


Figure 5. *Murraypneustes biannulatus* gen. et sp. nov. Detail of pore pairs and tubercles in and adjacent to ambulacrum V of paratype, NMV P312372.

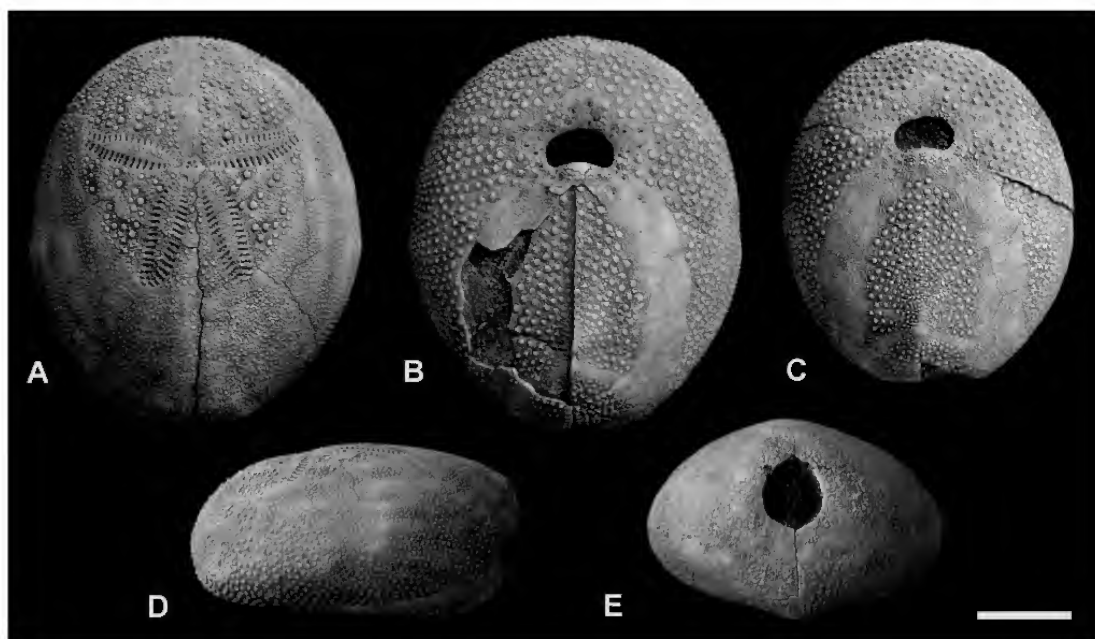


Figure 6. *Spatagobrius dermodyorum* sp. nov. A, B, D, adapical, adoral, and left lateral views of holotype, NMV P312570; C, adoral view of paratype, NMV P312571; E, posterior view of paratype, NMV P312572. All specimens from the early Middle Miocene Glenforlan Formation in the vicinity of locality NMV PL3203, north of Blanchetown, South Australia. Scale bars 10 mm.

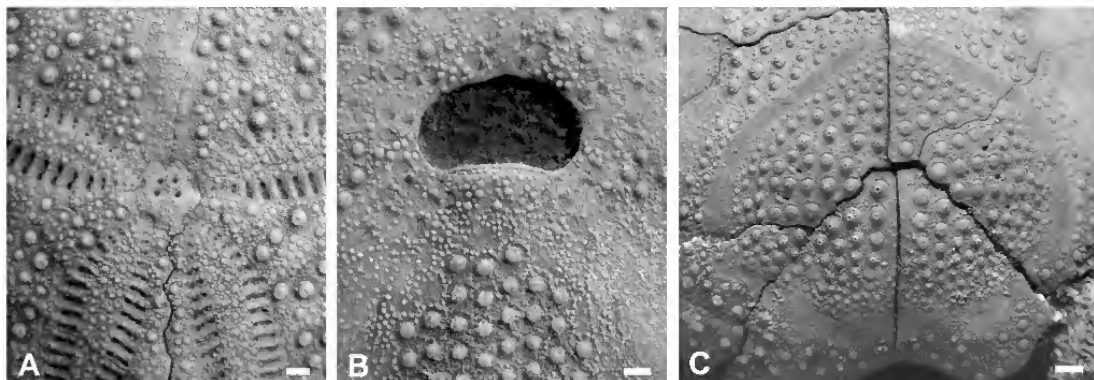


Figure 7. *Spatagobriissus dermodyorum* sp. nov. A, detail of petals and apical disk of holotype, NMV P312570; B, peristome and labrum tuberculation of paratype, NMV P312571; C, subanal fasciole and pore pairs of paratype, NMV P312573. Scale bars 1 mm.

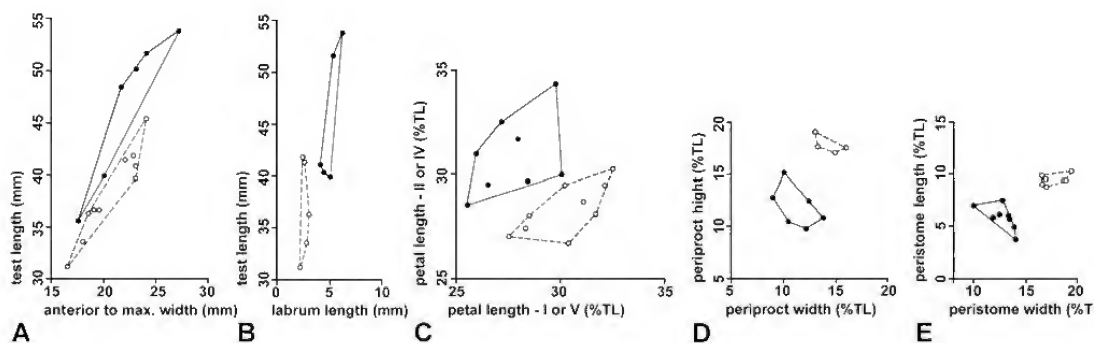


Figure 8. Comparative biometric data on specimens of *Spatagobriissus laubei* (Duncan, 1877) from the Middle Miocene Port Campbell Limestone, Port Campbell, Victoria (•), and *S. dermodyorum* sp. nov. from the early Middle Miocene Glenforslan Formation, Blanchetown district, South Australia (o).







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